RESEARCH ARTICLE

Between predators and parasitoids: Complex interactions among shelter traits, predation and parasitism in a shelter-building caterpillar community

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Abstract

1. Shelter-building is widespread in the animal world and such shelters often influence the success of their builders. Shelters built by caterpillars influence the likelihood of attacks by natural enemies, but how particular shelter traits influence caterpillar survival is not known. Furthermore, the differential effects of certain shelter traits on some natural enemies, such as predators, may lead to 'enemy-free space' for other natural enemies (parasitoids). The parasitoid enemy-free space hypothesis has not been directly tested for shelter-building caterpillars.

2. To understand how shelter traits influence caterpillar survival, shelter traits, predation and parasitism were measured simultaneously for 24 caterpillar morphospecies (1,465 caterpillars) in a tropical dry forest and analysed in a phylogenetic context.

3. Shelter type, shelter openness and whether shelters accumulated frass had different amounts of phylogenetic signal, with frass accumulation displaying the most and shelter openness the least.

4. All three traits affected the frequency with which caterpillar species experienced predation. Predation was elevated in two shelter types (leaf folds and leaf rolls) compared to cut-and-fold shelters. Combinations of shelter openness and frass accumulation also affected predation, with closed frass-free shelters having the lowest predation and closed frass-filled shelters having the highest.

5. Parasitism was not affected by shelter traits but was strongly correlated with evolutionary history and negatively correlated with predation.

6. These results confirm a trade-off between predation and parasitism and demonstrate that predation can be more frequent than parasitism. Different shelter types result in different amounts of predation. These defensive shelter traits and their effectiveness also vary phylogenetically. Together, our results suggest that predation and parasitism determine the success of shelter-building caterpillars, and that success is a function of the specific shelter they construct. More generally, our results demonstrate the importance of considering the effects of defensive traits on both predators and parasitoids when investigating interactions between herbivores and natural enemies.

1 | INTRODUCTION

A wide variety of caterpillar traits have been shown to defend against predators and parasitoids (recently reviewed in Greeney, Dyer, & Smilanich, 2012; Zvereva & Kozlov, 2016). These studies have generally investigated morphological or chemical defences and have found that they decrease the success of predators and/or generalist parasitoids but are less effective against specialist parasitoids. A few studies have considered other potential defences, including immunological defences (Smilanich, Dyer, & Gentry, 2009) and behavioural defences (Gentry & Dyer, 2002; Sendoya & Oliveira, 2017). The general effectiveness of these latter types of defences is not well-understood.

One such behavioural defence is shelter-building by caterpillars. Although tens of thousands of caterpillar species from at least 25 families build shelters (Jones, 1999), most studies of caterpillar defences have focused on free-feeding caterpillars. When shelter-building caterpillars have been included, they have been compared as a group to free-feeding caterpillars (Connahs, Aiello, Van Bael, & Rodríguez-Castañeda, 2010; Diniz, Hay, Rico-Gray, Greeney, & Morais, 2012; Gentry & Dyer, 2002; Hrcek, Miller, Whitfield, Shima, & Novotny, 2013). These studies, as well as several experiments in which shelter-building caterpillars have been exposed to natural enemies without their shelters (Covarrubias-Camarillo, Osorio-Beristain, Legal, & Contreras-Garduño, 2016; Jones, Castellanos, & Weiss, 2002; Sendoya & Oliveira, 2017; Velasque & Del-Claro, 2016), demonstrate that caterpillar shelters in general affect the chances of predation and parasitism.

The question of how particular caterpillar shelters affect predation and parasitism has barely begun to be addressed. Caterpillar shelters can vary along at least four trait axes as follows: the materials used to build the shelter (here, all silk vs. leaves held in place by silk strands), the shape of the shelter (as a function of how the shelter materials are manipulated), the openness of the shelter to natural enemies and the distribution of frass within the shelter. Given the great diversity seen in these traits (Eiseman, Charney, & Carlson, 2010; Greeney & Jones, 2003; Weiss, 2003), it is unlikely that all shelters or all shelter traits are equally effective against all predators and parasitoids, although little is known about this. In one instance, hesperiid caterpillars resting on the ceilings of open shelters have been reported to be undisturbed by ants passing directly below them (H. F. Greeney, pers. comm.), but such a strategy seems unlikely to be effective against larger or more visual predators such as spiders or wasps (Jones et al., 2002). Furthermore, there may be a trade-off between defending against predators and defending against parasitoids. Comparisons between shelter-building and free-feeding caterpillars suggest that shelter-building generally increases parasitism (Connahs et al., 2010; Gentry & Dyer, 2002; Hrcek et al., 2013; but see Diniz

et al., 2012). These investigators propose that shelter-building caterpillars experience less predation than free-feeding caterpillars, and as a result are more likely to experience higher parasitism because the parasitoids seek safer hosts, that is, ones that will not be eaten by predators. If this is the case, shelter-building caterpillars would serve as enemy-free space for the parasitoids (Jeffries & Lawton, 1984; Murphy, Lill, Bowers, & Singer, 2014; Stireman III, O'Hara, & Wood, 2006). This prediction has not been tested directly because measuring predation on free-feeding caterpillars in natural settings is exceedingly difficult (e.g. securing larvae to the substrate is probably required: Steward, Smith, & Stephen, 1988). However, predation is easier to measure for shelter-building caterpillars because shelter-building caterpillars do not move as much as free-feeding species and the shelter itself marks the position of the individual caterpillar. If shelter differences affect the predation of shelter-building caterpillars, then the predictions of the parasitoid enemy-free space hypothesis could be tested within a community of shelter-building caterpillars.

We addressed the questions of how caterpillar shelters affect predation and parasitism and whether there is a negative correlation between predation and parasitism using 24 species of caterpillars in the tropical dry forest of Palo Verde National Park, Costa Rica. For each species, we measured shelter traits, predation and parasitism. Because these caterpillars came from multiple families, we also collected genetic data so that we could analyse the effectiveness of these shelter traits in an evolutionary context. We used these data to test both the hypothesis that shelter traits differentially affect predation and parasitism and the parasitoid enemy-free space hypothesis.

We hypothesized that shelter type, shelter openness and the level of frass accumulation would contribute to the likelihood of predation. Shelters at Palo Verde can be divided into five general types (webs, leaf folds, leaf rolls, leaf ties or cut-and-fold shelters; see Figure 1) that differ in basic materials, shapes and construction methods. Web shelters consist of quantities of silk attached to host plant substrates, while the other shelter types are formed by manipulating leaves with silk. We predicted that predation would vary among shelter types. Because there is very little information about how different predators interact with caterpillar shelters or the Palo Verde predator community, we did not try to predict which shelter types would be associated with higher predation. We predicted that predation would be higher in open shelters than closed shelters, due to their greater accessibility, and that open shelters with frass would have the highest predation, as frass has been shown to attract predators (Moraes, Greeney, Oliveira, Barbosa, & Freitas, 2012; Weiss, 2003). In accordance with the parasitoid enemy-free space hypothesis (Murphy et al., 2014), we predicted that parasitism and predation would be negatively correlated, and that shelter factors

$\lambda = 0.75$
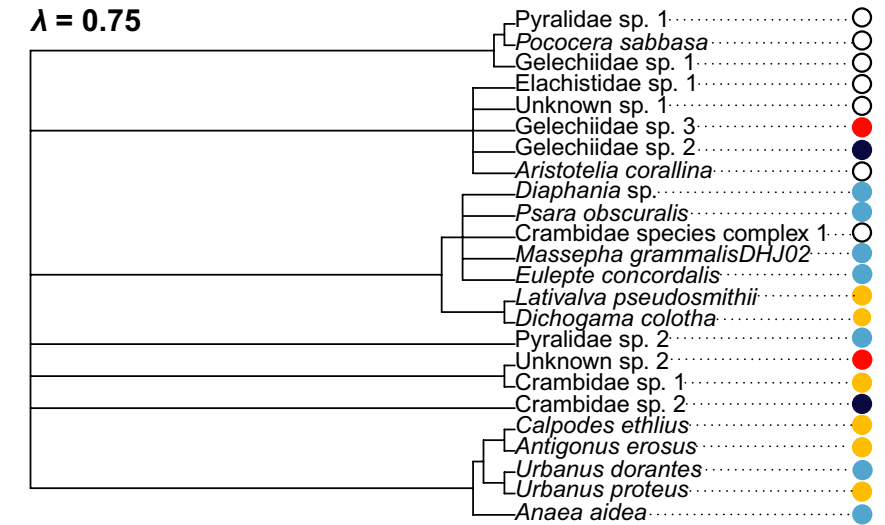
FIGURE 1 Focal species' shelter types mapped onto the ultrametric phylogeny. Shelter exemplars: cut-and-fold shelter (Crambidae sp. 1), leaf fold (*Diaphania* sp.), leaf roll (Crambidae sp. 2), leaf tie (Unknown sp. 2) and web (*Aristotelia corallina*). Colours indicate shelter types
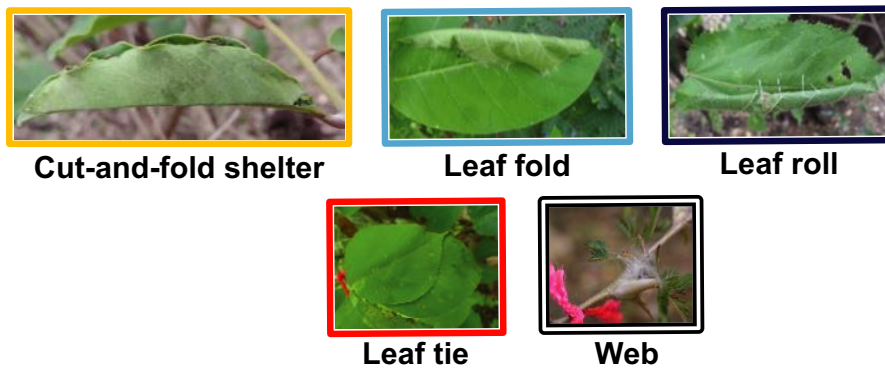
associated with low predation would be associated with high parasitism.

2 | MATERIALS AND METHODS

2.1 | Study site and organisms

The research was conducted in Palo Verde National Park, Guanacaste, Costa Rica, in the area around Palo Verde Biological Station (PVBS; 10°21′N, 85°21′W). PVBS is surrounded by low elevation (0–200 m) secondary tropical dry forest and is adjacent to a large seasonal wetland. Fieldwork was performed from late May to early August 2014–2016, during what is normally the first part of the wet season.

Focusing on 24 morphospecies of shelter-building caterpillars, we monitored a total of 1,033 caterpillars in the field to measure predation and collected at least 20 individuals per morphospecies (total: 955; $M \pm SE$: 39.8 ± 6.1) to measure parasitism (Table 1). One morphospecies (Crambidae species complex 1) consists of three species. While the adults are readily distinguishable, their caterpillars and shelters are not. They are more closely related to each other than to any of the other species and they are analysed as a species complex here because caterpillars lost to predators could not be identified to species.

2.2 | Field methods

We searched for caterpillar shelters primarily along roads, human- and animal-made trails and natural edges, as these areas had the most accessible foliage. We visually scanned foliage from ground level to ~3 m for shelters and feeding damage. Caterpillar shelters found in the field were checked for inhabitants by backlighting them with a hand-held light. Inhabited shelters were marked, photographed and their dimensions measured to the nearest millimetre. The length of the caterpillar was also measured. Caterpillars were collected when we estimated that they were at least half-grown. The original size cut-off used was 15 mm, as this corresponded to third instar caterpillars for common Palo Verde hesperiids (e.g. *Calpodes ethlius*, *Urbanus dorantes* and *U. proteus*). However, as many microlepidopteran caterpillars never reached 15 mm or reached it much later in development, those species were collected when they reached 10 mm in length. If a caterpillar was estimated to be less than half-grown, we checked it each day until it either reached that size or had been monitored for 6 days, at which time it was collected.

At each daily check, we located the caterpillar, measured it and confirmed its survival by checking for new feeding damage and caterpillar movement using backlighting. We also documented any new shelters built by the caterpillar. If we could not find a caterpillar in its shelter, we searched the plant and any touching conspecific plants for the caterpillar. If at least 2 days passed without locating

TABLE 1 Shelter-building morphospecies used in this study. 'Undescribed' means that a species matches an established DNA barcode, but that the specimens corresponding to that barcode have not been described or given a single working name. Shelter type: CF: cut-and-fold shelter, F: leaf fold, R: leaf roll, T: leaf tie, W: web. Y = Yes, N = No

Morphospecies reference name	Family	Species	Host plant family	Shelter type	Open	Frass	Predation N	Parasitism N
Calpodes ethlius	Hesperiidae	Calpodes ethlius	Marantaceae	CF	Y	N	19	35
Urbanus dorantes	Hesperiidae	Urbanus dorantes	Fabaceae	F	Y	N	47	55
Urbanus proteus	Hesperiidae	Urbanus proteus	Fabaceae	CF	Y	N	14	21
Psara obscuralis	Crambidae	Psara obscuralis	Petiveriaceae	F	Y	N	45	29
Lativalva pseudosmithii	Crambidae	Lativalva pseudosmithii	Capparaceae	CF	N	Y	18	24
Crambidae sp. 1	Tentatively Crambidae	Not previously barcoded	Capparaceae	CF	N	Y	26	26
Gelechiidae sp. 1	Gelechiidae	Undescribed	Fabaceae	W	N	Y	69	30
Pyralidae sp. 1	Pyralidae	epipaJanzen01 Janzen15DHJ02	Polygonaceae	W	Y	Y	45	39
Diaphania sp.	Crambidae	Diaphania Dapkey02	Apocynaceae	F	N	Y	55	45
Gelechiidae sp. 2	Gelechiidae	Undescribed	Combretaceae	R	Y	N	34	33
Massepha grammalis	Crambidae	Massepha grammalisDHJ02	Marantaceae	F	N	Y	25	36
Eulepte concordalis	Crambidae	Eulepte concordalis	Bignoniaceae	F	Y	Y	37	32
Crambidae sp. 2	Tentatively Crambidae	Phaedropsis Janzen10	Malvaceae	R	Y	Y	42	36
Antigonus erosus	Hesperiidae	Antigonus erosus	Malvaceae	CF	Y	N	34	32
Pyralidae sp. 2	Tentatively Pyralidae	chryJanzen01 Janzen347	Solanaceae	F	Y	N	40	31
Unknown sp. 1	Gelechiidae/ Elachistidae	Undescribed	Polygonaceae	W	N	N	29	28
Anaea aidea	Nymphalidae	Anaea aidea	Euphorbiaceae	F	Y	N	45	36
Unknown sp. 2	Unidentified	Not previously barcoded	Capparaceae	T	Y	Y	51	32
Dichogama colotha	Crambidae	Dichogama colotha	Capparaceae	CF	N	Y	10	41
Elachistidae sp. 1	Elachistidae	elachJanzen01 Janzen737	Primulaceae	W	N	Y	21	40
Pococera sabbasa	Pyralidae	Pococera sabbasaJanzen02	Fabaceae	W	N	Y	158	176
Aristotelia corallina	Gelechiidae	Aristotelia corallina complex	Fabaceae	W	N	N	33	29
Crambidae species complex 1	Crambidae	Syllepte belialis Chilochromopsis sceletogramma Pilocrocis calamistis	Salicaceae	W	Y	N	38	30
Gelechiidae sp. 3	Gelechiidae	Unidentified	Fabaceae	T	N	Y	98	39

the caterpillar, the caterpillar's disappearance was recorded as occurring the day after it was last seen and all shelters were collected. As shelter-building caterpillars spend nearly all their time in or near their shelters, the disappearance of a caterpillar was assumed to represent a predation event. While some caterpillar species disperse prior to pupation, caterpillars were too young for this to be a cause of disappearances during field monitoring. Any evidence of predation was recorded, including damage to the shelter, a predator attacking a caterpillar or a predator in or near the shelter. If a dead caterpillar was found in a shelter or there was evidence of parasitoid emergence from a caterpillar, the shelter and its contents were immediately collected.

Surviving caterpillars were reared in an ambient air laboratory at PVBS inside their shelters in plastic bags. To maintain the foliage, stems were placed in individual florists' tubes filled with water. Fresh foliage was added as needed and caterpillars were checked daily for new shelters, ecdysis, pupation, eclosion and parasitoid emergence.

Old shelters were collected and characterized once they were no longer in use.

2.3 | Shelter characteristics

Shelters were photographed from multiple angles after collection or when newly built in the laboratory. In addition to this documentation, several shelter characteristics were recorded for each shelter: shelter type, whether the shelter was open or closed (we define 'open' as having openings larger than 2 mm × 2 mm), and whether frass accumulated in the shelter. We identified five shelter types: web, leaf tie, leaf fold, leaf roll and cut-and-fold shelter (Figure 1). Webs are shelters constructed primarily with silk attached to leaves or other plant parts for support. Leaf ties are two or more leaves sandwiched together with silk. Leaf folds are single leaves folded once, while leaf rolls are rolled in on themselves multiple times. Cut-and-fold shelters are built by cutting a leaf flap and pulling it over the rest of the leaf with silk. Some caterpillar species build multiple shelter types as they become larger and can manipulate leaves in different ways. In these cases, we used the shelter type built by all young caterpillars.

2.4 | Laboratory methods and identification

All dead caterpillars and pupae were dissected to check whether they contained parasitoid larvae that had not emerged. Caterpillars, lepidopteran adults and parasitoids were identified with *cox1* DNA barcoding using the methods described in Baer (2018). Two nuclear genes, *EF1-α* and *wg*, were also amplified using primers from Cho et al. (1995) and Brower and DeSalle (1998) and PCR methodologies based on those of Wahlberg and Wheat (2008) (see Appendix S1 for detailed methods).

2.5 | Phylogenetic reconstruction and statistics

All insect species were identified via barcoding, and all host plant species were identified by comparing field-collected voucher specimens with herbarium specimens (MO). The gene sequences for the Palo Verde caterpillar species were combined with *cox1*, *EF1-α* and *wg* sequences from the 2010 phylogeny by Mutanen and colleagues containing all lepidopteran clades. Each gene was aligned individually in AliView (version 1.18.1; Larsson, 2014) using MUSCLE (Edgar, 2004) and then checked by eye. Individual gene trees were then generated using RAxML (Stamatakis, 2014) through the CIPRES Science Gateway (Miller, Pfeiffer, & Schwartz, 2010), using *Micropterix calthella* (Micropterigidae) as an outgroup. After the gene trees were examined, the genes were concatenated in Mesquite (Maddison & Maddison, 2017). A species tree was generated in RAxML using the partitioned three-gene matrix and an initial tree constraining the families supported by the full eight-gene Mutanen, Wahlberg, and Kaila (2010) tree to monophyly. For Palo

Verde taxa, a morphospecies was constrained if it had been identified as a described species belonging to that family, but not if the species had only been tentatively identified as belonging to that family. When the resulting tree was examined, we found that the Mutanen et al. (2010) taxa near the focal taxa did not provide additional information about how the focal taxa were related to each other. Accordingly, these additional taxa were removed except for *M. calthella* and *Agathiphaga queenslandensis* (Agathiphagidae), which were kept as outgroups. A smaller tree was then generated using this partitioned dataset, again constrained so that shelter-building morphospecies which had been identified to species in two families supported by the full Mutanen et al. (2010) phylogeny (Crambidae and Hesperiidae) would be monophyletic. This final tree was made ultrametric in R (R Core Team, 2016) using the APE package (Paradis, Claude, & Strimmer, 2004).

All phylogenetic least squares (PGLS) analyses were performed in R using APE. A species' parasitism was expressed as the proportion of parasitized individuals in all the collected caterpillars (percent parasitism). Predation was expressed as the proportion of predation events during the number of monitored caterpillar-days (the daily predation rate). For shelter traits, shelter type was treated as an unranked categorical variable, while openness and frass accumulation were binomial variables. Some focal species build different shelters depending on caterpillar age or host plant characteristics; in these cases, shelter traits were drawn from the shelter built by all young caterpillars while they were exposed in the field.

The relationships between the different shelter traits (type, openness and frass accumulation) and the effect of phylogeny were analysed by modelling each trait as a dependent variable predicted by the other two. In each case, Pagel's lambda was calculated to measure phylogenetic signal. A Pagel's lambda value of 0 indicates no phylogenetic signal, while values near 1 indicate that traits are distributed across the phylogeny in a manner consistent with a Brownian motion model of evolution (Pagel, 1999). Interactions between frass accumulation and openness were tested, but potential interactions between shelter type and the other variables could not be analysed as some combinations of shelter type and openness or shelter type and frass accumulation were not present in the dataset. Parasitism and predation were modelled separately using the three shelter traits as independent variables and Pagel's lambda was calculated in each case. Because the dependent variables were proportions, they were logit-transformed (Warton & Hui, 2011). The correlation between parasitism and predation was also calculated. All data and code for these analyses are archived in the Dryad Digital Repository (Baer, Morales Gutierrez, & Marquis, 2020).

2.6 | The uncertainties of estimating predation and parasitism in natural systems

Estimating predation and parasitism in complex natural systems is difficult and time-consuming. As in any field methodology, there

was some uncertainty that could not be completely resolved. Most of this uncertainty concerns the fates of the caterpillars that disappeared. The available literature (Libra, Tulai, Novotny, & Hrcek, 2019; Loeffler, 1996) and all our observations indicate that shelter-building caterpillars are quite sedentary. We saw many free-feeding caterpillars hanging from silk lines or travelling rapidly over bare earth or branches, but we never saw shelter-building species outside their shelters unless they were feeding or building. On the ground, herbivorous insects without physical defences are an easy prey for predators (Castellanos & Barbosa, 2011; Losey & Denno, 1998). Additionally, a shelter-builder feeding on a small plant would usually defoliate the original plant before moving to another, even if a second host plant was touching the first. Furthermore, when we found older caterpillars, their shelters either had signs of long-term occupation or were next to ontogenetic series of previous shelters. Finally, because we were monitoring sets of known caterpillars, the only way we could misidentify individual caterpillars was if they were in close proximity, of the same species and size, and therefore analogous for the purposes of our study. This situation rarely happened. Based on all these considerations, we believe that we were able to accurately track caterpillar movements within and between neighbouring plants and that young shelter-building caterpillars rarely engage in long-distance dispersal across multiple plants. Therefore, we are quite confident that most of the caterpillar disappearances we observed were caused by predation.

A second question regarding the vanished caterpillars is how many of them had been attacked by parasitoids. There are various reasons to hypothesize that parasitized caterpillars would be either more or less vulnerable to predators than unparasitized caterpillars (Stamp, 1981). Our personal observations lead us to believe that parasitized shelter-building caterpillars at Palo Verde are less likely to be killed by predators than unparasitized caterpillars, as many of them become less active, remain in their shelters even if they normally feed outside and even seal normally open shelters. To test how sensitive our parasitism estimates from the collected caterpillars were to caterpillar disappearances, we compared parasitism estimates under four different scenarios. Scenario 1 was the original estimate, which excluded the caterpillars that disappeared. Scenario 2 assumed that parasitized caterpillars completely avoid predation and assigned all vanished caterpillars to the 'unparasitized' category. Scenario 3 assumed that parasitized and unparasitized caterpillars were equally vulnerable to predators and assigned half to each category. In the case of an odd number of missing caterpillars, the odd one was arbitrarily assigned to unparasitized. Finally, Scenario 4 assumed that parasitized caterpillars were completely vulnerable to predators and all missing caterpillars were considered parasitized. Scenario 2 and Scenario 4 represent the lowest and highest parasitism levels possible, respectively.

After these projected counts were calculated for all species and scenarios, we used a generalized linear model to test whether the numbers of parasitized and unparasitized caterpillars were dependent on caterpillar species, scenario, or the interaction between the two.

3 | RESULTS

3.1 | Shelter traits

Shelter type (Pagel's $\lambda = 0.75$, Figure 1), shelter openness (Pagel's $\lambda = 0.45$) and frass accumulation (Pagel's $\lambda = 1.04$) all showed a significant effect of phylogeny, with the strongest effect of phylogeny on frass accumulation. After controlling for the effect of phylogeny, shelter openness was correlated with shelter type (leaf rolls are more likely to be open than other shelter types, $p = 0.044$) and frass accumulation (frass-containing shelters were less likely to be open, $p = 0.012$). In turn, frass accumulation was also associated with shelter type: webs and leaf rolls were less likely to accumulate frass than the three other shelter types ($p = 0.032$ and 0.045 respectively).

3.2 | Predation

Species' daily predation rates ranged from 1.7% to 29.9% (Figure 2). There was some phylogenetic signal for predation (Pagel's $\lambda = 0.49$). Shelter type, frass accumulation and the interaction between shelter openness and frass accumulation were significant predictors of the remaining variation in predation (Table 2). Of the five shelter types, leaf folds and leaf rolls had significantly higher predation than cut-and-fold shelters) while leaf ties and webs had predation levels similar to cut-and-fold shelters (Table 3; Figure 3A). While shelter openness alone did not significantly affect predation, this result appears to be due to a negative interaction with frass accumulation (Table 2; Figure 3B). Open, frass-filled shelters experienced lower predation than would have been expected from the main effects alone (Table 3).

3.3 | Parasitism

Parasitism for the different species ranged from 0% to 58.1% (Figure 2), with very strong phylogenetic signal (Pagel's $\lambda = 1.04$). After controlling for phylogeny, none of the shelter traits had a significant effect on parasitism (Table 2). However, parasitism was negatively correlated with predation (Figure 4, $r = -0.60$, $p = 0.11$), a result consistent with the enemy-free space hypothesis. During the study, the proportion of caterpillars that escaped both predators and parasitoids was generally 50%–90% for each morphospecies.

The sensitivity analysis revealed that the parasitism estimates were robust to the variation created by the differential predation scenarios. The various scenarios did result in somewhat different parasitism estimates (Appendix S2, Table S1). However, only caterpillar species identity significantly affected parasitism in the GLM (Appendix S2, Table S2). Predation scenario had no effect, either directly or in combination with caterpillar species.
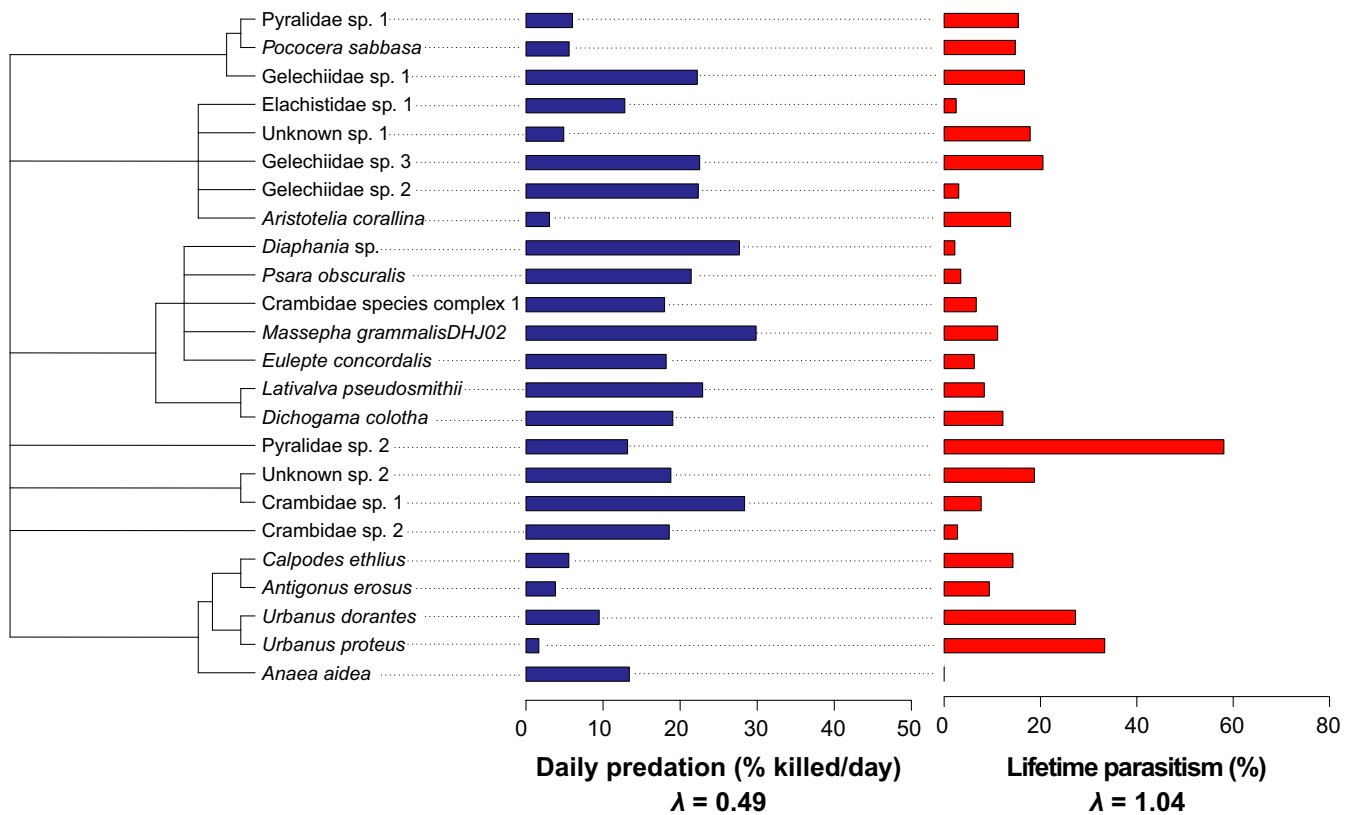
FIGURE 2 Predation and parasitism rates mapped onto the ultrametric phylogeny. Pagel's lambda indicates the strength of the phylogenetic signal

TABLE 2 ANOVAs for the phylogenetic generalized least squares regression of caterpillar predation, parasitism and shelter traits. Each dependent variable was logit-transformed before analysis. p values ≤0.05 are indicated in bold

Variable	Predation			Parasitism		
	df	F statistic	p value	df	F statistic	p value
Shelter type	4	3.260	**0.0390**	4	0.382	0.818
Shelter openness	1	5.271	**0.0355**	1	0.148	0.705
Frass accumulation	1	1.551	0.231	1	0.250	0.624
Openness × frass	1	6.501	**0.0214**	1	0.457	0.509

TABLE 3 Coefficients of the phylogenetic generalized least squares regression of caterpillar predation and shelter traits. p values ≤0.05 (in bold) indicate that a level's coefficient is significantly different from the reference level. Reference levels: shelter type = cut-and-fold shelter; shelter openness = closed shelter; frass accumulation = no accumulation

Variable	Coefficient	t statistic	p value
Shelter type: leaf fold	0.866	2.599	**0.0194**
Shelter type: leaf roll	1.403	2.295	**0.0356**
Shelter type: leaf tie	0.793	1.474	0.160
Shelter type: web	0.261	0.599	0.557
Open shelter	0.753	1.30	0.211
Frass accumulating shelter	1.47	2.74	**0.0146**
Openness × frass	−1.59	−2.55	**0.0214**

4 | DISCUSSION

Our sampling of 24 morphospecies from our Costa Rican dry forest site demonstrates that the shelters built by these caterpillars vary greatly in their size, shape, amount of silk, openness and frass accumulation. These shelter trait differences have a phylogenetic component (Figure 1), but the influence of phylogeny varied among traits, as did their correlations with other shelter traits. Shelter-building caterpillars also differed in predation and parasitism levels (Figure 2). Based on phylogenetically controlled analyses, these trait differences predict the likelihood of predation for the caterpillar that built the shelter (Figure 3). In turn, the results suggest that shelter traits also affected parasitism, but indirectly, because parasitoids avoid caterpillar species that are likely to be killed by predators (Figure 4). Together, these results support our first hypothesis that caterpillar shelters vary in their effectiveness as defences against
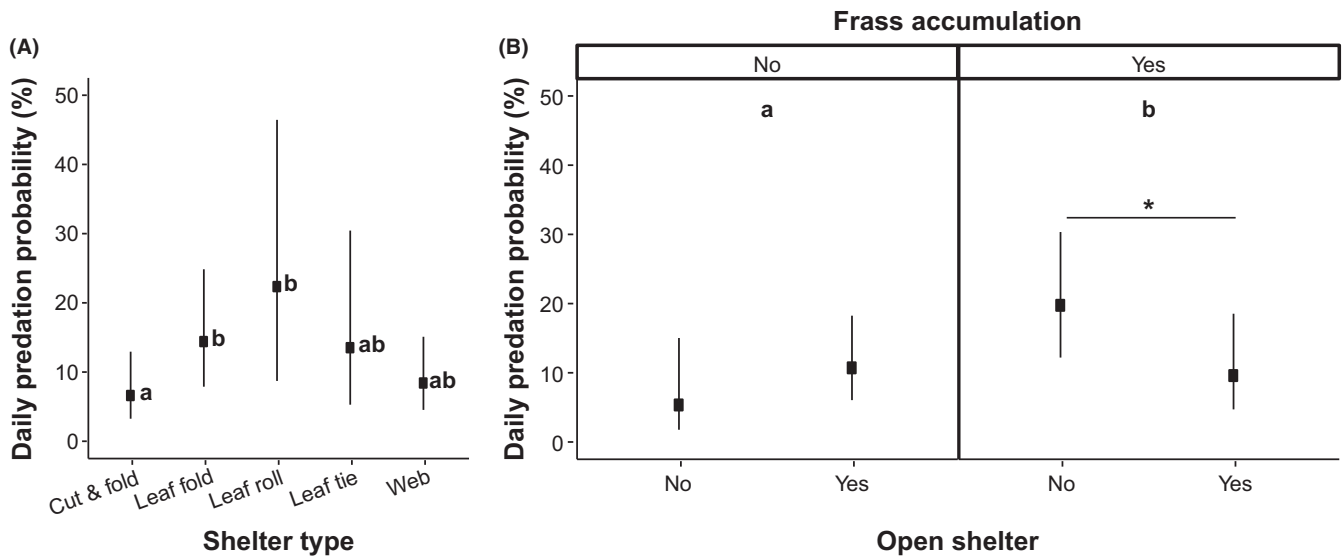
FIGURE 3 Effects of shelter traits on caterpillar predation probability. Effect estimates (±95% confidence intervals) are back-transformed from the logistic model. (A) Shelter type affects predation. Different letters indicate statistically different groups. (B) Frass accumulation and shelter openness have interacting effects on predation. Different letters and the asterisk indicate statistically significant differences
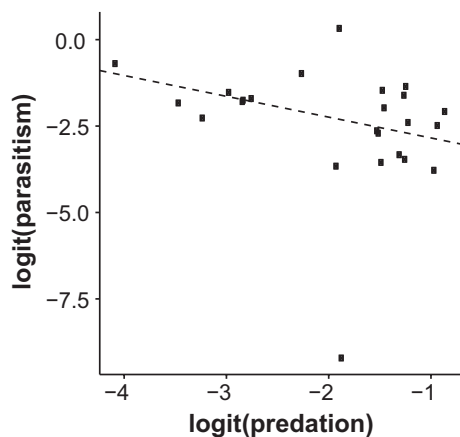
FIGURE 4 Phylogenetically controlled correlation of logistically transformed predation and parasitism data

natural enemies. This means that caterpillar shelters should not be treated as single category in studies of the ecology and evolution of caterpillar defences. In fact, there is as much variation in predation and parasitism levels among these 24 species of shelter-building caterpillars as there is for non-shelter building caterpillars that vary in chemical and physical defences (e.g. Gentry & Dyer, 2002; Murphy et al., 2014). Finally, our analysis supports the parasitoid enemy-free space hypothesis, as there was a negative correlation between parasitism and predation.

4.1 | The phylogenetics of shelter building

Caterpillar shelters have been suggested to be phylogenetically informative within families (Greeney & Jones, 2003), and it has long been recognized that different lepidopteran families build shelters with different architectures and materials (Jones, 1999; Stehr, 1987). However, to our knowledge, caterpillar shelters have not been previously mapped onto a phylogeny. Although our phylogeny (Figure 1) is incompletely resolved and includes a subset of the entire Palo Verde shelter-building community, it raises several interesting points. First, the web shelter type is built by members of each of the three clades corresponding to the Crambidae, Gelechioidea and Pyralidae. The only large lepidopteran clade in our sample that does not include a web-builder is the Hesperiidae + Nymphalidae clade, but some nymphalid caterpillars build webs (DeVries, 1987; Stamp, 1982; Wynter-Blyth, 1957). This suggests that web-building is, if not the basal shelter type, the most phylogenetically widespread one. Second, this analysis suggests some intrafamilial patterns worthy of further study. The two previously described crambid species that build cut-and-fold shelters appear separate from the others, raising the question of how cut-and-fold shelters are distributed within the Crambidae. Within the Hesperiidae, the two species from the polyphyletic *Urbanus* genus (Pfeiler, Laclette, & Markow, 2016) build different types of shelters, suggesting that the shelter traits of other species in the group may be phylogenetically informative. The shelters built by our focal species are consistent with previously reported family-level shelter associations (Jones, 1999; Stehr, 1987). However, the literature offers few treatments of species' shelters, with shelter-building hesperiid caterpillars better represented than those of other families (Greeney, 2009; Greeney & Jones, 2003). Mapping shelter types onto more complete phylogenies and sampling many more species will certainly give further insights into the evolution of shelter-building.

There was substantial variation in phylogenetic signal for different shelter traits. Frass accumulation showed the strongest phylogenetic signal, while shelter openness showed the least. The strong phylogenetic signal for frass accumulation may be because frass-free

shelters are frequently the result of morphological structures that allow caterpillars to excrete frass at high velocities. While these anal structures are not limited to shelter-building caterpillars, they occur in the Gelechiidae, Hesperiidae, and Nymphalidae (Weiss, 2003), and 8 of the 11 focal species that build frass-free shelters belong to these families. By contrast, shelter type and openness depend on caterpillar behaviours and host plant characteristics and may be more evolutionarily labile.

4.2 | Predation and shelters

This study demonstrates that shelter traits affect predation across a wide range of distantly related shelter-building species. In this community, leaf folds and rolls experience higher predation than cut-and-fold shelters, while leaf ties and webs do not (Figure 3A). Further study is needed to determine whether this holds true in other shelter-building communities and why the former shelter types are more vulnerable. The effect of shelter openness and frass accumulation on predation also shows that shelter traits can have interacting effects on predation (Figure 3B). Contrary to our prediction, the highest predation occurred in closed shelters that accumulate frass, while the lowest predation occurred in closed, frass-free shelters. (Closed, frass-free shelters occur when caterpillars either open and close the shelter for each defaecation or expel frass through openings that were smaller than our 2 mm × 2 mm threshold.) Predation was influenced by frass accumulation but shelter openness only significantly affected predation in frass-accumulating shelters. Frass has been shown to attract predators to open shelters (Moraes et al., 2012; Weiss, 2003), but no behavioural experiments have been performed with predators and closed shelters. As many closed shelters are closed using frass embedded in silk, the associated volatiles may increase shelter apparency. These shelters appeared undamaged, so predators presumably attacked when caterpillars exited the shelters to feed, perform maintenance or build a new shelter.

To better understand how shelter traits affect predation, more information about the predators is needed. During the study, the most commonly observed predators of shelter-building caterpillars were actively hunting spiders (particularly the green lynx spider, *Peucetia viridans*: Family Oxyopidae) and predatory wasps. Although ants and predatory hemipterans are known to attack free-feeding caterpillars at Palo Verde (Dyer, 1997), they were rarely observed attacking or feeding on shelter-building caterpillars in this study. Ants in a Brazilian cerrado community rarely attacked caterpillars inside their shelters (Sendoya & Oliveira, 2017), so ants may be more important predators of free-feeding caterpillars. Mantids and orthopterans were also occasionally observed in or near the shelters of vanished caterpillars, and may have caused those disappearances, but they were never caught in the act of predation. These observations suggest that the vast majority of predators were invertebrates. Only one probable case of vertebrate predation was observed, in which large holes were torn in a web to reach the caterpillar's

resting site. Vertebrate bite damage to leaf shelters as described by Tvardikova and Novotny (2012) was never observed. These results are consistent with several artificial caterpillar experiments that found that most predation attempts in lowland tropical forests were made by invertebrates (Loiselle & Farji-Brener, 2002; Richards & Coley, 2007; Roslin et al., 2017; Sam, Koane, & Novotny, 2015; Solis-Gabriel, Mendoza-Arroyo, Boege, & Del-Val, 2017; Tvardikova & Novotny, 2012).

Natural caterpillar predation rates have rarely been measured directly in the field, as monitoring the survival of freely moving caterpillars is challenging. Accordingly, much of what is known about the frequency of caterpillar predation comes from experiments with artificial caterpillars such as those mentioned above, and studies that assess the caterpillar preferences of specific predators (e.g. Dyer, 1997; Dyer & Floyd, 1993; Janzen, 1987; Murphy, Leahy, Williams, & Lill, 2010; Roslin et al., 2017; Sendoya & Oliveira, 2017; Tvardikova & Novotny, 2012). Directly measuring predation of caterpillars in the field is facilitated by shelter-building, because a shelter serves as both a record of the caterpillar's presence and the caterpillar's centre of activity. While tracking a shelter-building caterpillar from day to day is easier than tracking a free-feeding one, some shelters can be more difficult to monitor than others. This was particularly true of leaf-rolling species in this study (Gelechiidae sp. 2 and Crambidae sp. 2), whose continued presence often had to be assessed using feeding damage or changes to the shelter structure, rather than direct observation of the caterpillar. The disappearance of some caterpillars may also be more complicated than simple predation, as caterpillars can fall from their plants while seeking new shelter sites (Loeffler, 1996; Sliwinski & Sigmon, 2013). Although these caterpillars are not removed from the plant by predators, they can be killed by terrestrial predators before they can return to the plant (Sliwinski & Sigmon, 2013). Despite these complications, shelter-building caterpillars offer an excellent opportunity to directly measure predation in the field. These measurements can explore predation at a community level, as well as compare common predation estimates (artificial caterpillars or predator attack trials) to natural predation rates.

4.3 | Parasitism, shelters and predation

We were able to robustly estimate parasitism, as demonstrated by our parasitism projections comparing various differential predation scenarios for parasitized and unparasitized caterpillars. These different scenarios did not significantly affect the parasitism estimates either independently or through species-specific interactions. This analysis supports our conclusion that there was no evidence that shelter traits influenced parasitism. This result contradicted our original prediction that the same shelter traits would affect both predation and parasitism. Instead, parasitism was strongly predicted by evolutionary history. Despite this, when we controlled for evolutionary history, there was a negative correlation between parasitism and predation, the latter being influenced by shelter traits.

There are at least three possible explanations for this negative relationship between predation and parasitism, although the first two seem unlikely for our study. First, the correlation between parasitism and predation could be indirect: parasitism could be driven by another caterpillar trait that is negatively correlated with predation. For instance, caterpillar immune responses to implanted objects have been shown to be better predictors of parasitism than the morphological and behavioural factors previously identified in the same community (Gentry & Dyer, 2002; Smilanich et al., 2009). If parasitism at Palo Verde is primarily driven by caterpillars' immunological defences, parasitoids would still seek enemy-free space, but the relevant caterpillar trait would be the caterpillar's immune system. However, any relationship between caterpillar species' immune responses and predation has not been investigated. There is also no expectation that immune responses and predation would be negatively correlated.

Second, parasitism could be negatively correlated with predation due to non-shelter traits that influence both but in opposite directions, such as chemical or morphological defences, which have been shown to influence parasitism and predation in free-feeding caterpillars (Dyer & Floyd, 1993; Gentry & Dyer, 2002; Murphy et al., 2010, 2014). Although all caterpillar species used in this study appeared glabrous and non-aposematic to the human eye, no systematic observations of predators or parasitoids interacting with them have been made. These caterpillars also feed on host plants from 14 different families (Table 1) with diverse secondary chemistries. Whether these compounds influence predation and/or parasitism is unknown; the caterpillars seem to be palatable to generalist predators.

Third, and most probably, shelter traits may influence parasitism mainly through their effects on predation. These effects may be further complicated by the fact that some caterpillar species produce shelters that differ with caterpillar instar. Although our analysis did not fully account for this ontogenetic variation, or its effects on predation risk, parasitoids are experiencing those predation risks in their full complexity. Indirect shelter effects through predation cannot be currently tested with path analysis because the morphospecies sample size is too small. Future research could address these three alternative hypotheses by collecting data on the immunological, morphological and chemical acceptability of more caterpillar species and analysing the interactions between those traits, phylogeny, predation and parasitism.

Regardless of the underlying reasons for the negative correlation between predation and parasitism in this community, this study provides support for the parasitoid enemy-free space hypothesis (Murphy et al., 2014), which proposes that parasitoids prefer hosts that are less likely to be killed by predators. To our knowledge, this study is the first to simultaneously quantify both predation and parasitism for a set of caterpillar species with a range of defences, although other studies have shown that gradients of differentially effective defence traits can affect either parasitism or predation in contrasting directions (e.g. Dyer & Floyd, 1993; Gentry & Dyer, 2002; Murphy et al., 2010, 2014). Our results support the hypothesis that

differences in the predator-free space provided by different caterpillar species drives differences in parasitism.

The large differences in predation and parasitism for different shelter-building caterpillar species raise the question of how meaningful broad feeding strategy classifications such as 'shelter-builder' are for predicting parasitism or predation. This question is difficult to answer because many large-scale parasitism studies do not estimate parasitism for individual caterpillar species and therefore cannot quantify the variation within feeding strategy groups (but see Hrcek et al., 2013). The caterpillar species in our study had a wide range of parasitism (0%–58%), as did the shelter-building caterpillar species from Papua New Guinea (0%–40%, Hrcek et al., 2013). Parasitism of free-feeding caterpillar species in Papua New Guinea was less variable (0%–15%), although this could also result from a smaller sample size (six free-feeding species vs. 32 shelter-builders). The variation in parasitism for another set of free-feeding caterpillars was comparable to that of shelter-builders (25%–65%, Murphy et al., 2014). Further tests of the parasitoid enemy-free space hypothesis in these and other caterpillar communities could be performed by comparing predation and parasitism at the species level for multiple species of free feeders and shelter-builders, rather than comparing the two groups en masse.

More broadly, caterpillar shelters can be conceptualized as constructed niches (modifications of the biotic and abiotic environment) that result from heritable behaviours of the constructor. This niche construction in turn creates unique selection pressures for the constructing organism (Odling-Smee, Laclette, & Markow, 2003). Under the framework of niche construction, caterpillar shelters can be compared to a wide range of defensive structures, from nests and burrows (e.g. Rand & Host, 1942; Ricklefs, 1969; Weber, Peterson, & Hoekstra, 2013) to external shells (e.g. Boulding, 1984; Vermeij, 1977) and plant galls (Weis & Abrahamson, 1986).

Unlike many of these constructed niches (e.g. bird nests and external shells), however, there does not appear to be a clear relationship between the complexity of caterpillar shelters and their effectiveness against predation or parasitism. For instance, leaf rolls are more structurally complex than leaf folds, but in this study both experienced similar and relatively high predation. This may change as the effects of caterpillar shelters on predation and parasitism become more widely measured, but it may also reflect the unique challenges of defending against predators and parasitoids. Compared to pathogens and parasites, which reproduce within their hosts and have opportunities to be successfully transmitted to new hosts before (or even during) host predation, parasitoids are under intense selection to choose hosts that will not be killed before the parasitoid has completed its development (Lafferty & Kuris, 2002). Gall-inducing insects are also targeted by predators and parasitoids, and Weis and Abrahamson (1986) found that these two guilds exerted opposing pressures on gall-makers, with the overall direction of selection on a population dependent on the relative abundance of predators and parasitoids at a particular time. Our evidence suggests that shelter-building caterpillars are performing a similar

balancing act while defending themselves against predators and parasitoids.

5 | CONCLUSIONS

Simultaneously quantifying predation, parasitism and potential defensive traits for multiple prey species can offer significant insights about the functional traits that influence natural enemy–prey interactions in a community. We show here that predation can be predicted by shelter traits and that predation is negatively correlated with parasitism across a wide range of species. As shelter-building caterpillars are often the most abundant caterpillars (Diniz et al., 2012; Hrcek et al., 2013), and sometimes the most abundant insect herbivores (Lill & Marquis, 2007) in communities, these results suggest that shelters will determine which predators will attack which caterpillars and how heavily different caterpillar species are preyed upon. Meanwhile, the negative relationship between predation and parasitism provides support for the parasitoid enemy-free space hypothesis. Such a relationship between predation and parasitism not only has the potential to explain many of the patterns found in caterpillar communities, but can also inform management decisions, including whether non-native or pest caterpillars (many of which are shelter-builders, Lill & Marquis, 2007) would be more vulnerable to predators or parasitoids. Such differences could guide searches for biological control agents. Different caterpillar shelters are not the same when it comes to providing protection from predators and parasitoids. These differences likely have ramifications for community structure and functioning for at least three trophic levels, both in natural and more managed ecosystems.

AUTHORS' CONTRIBUTIONS

C.S.B. and R.J.M. designed the experiment; C.S.B. collected and analysed the data; C.S.B. led the writing of the manuscript and R.J.M. contributed revisions and suggestions.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.