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SEASONAL DYNAMICS OF LEAF-TYING CATERPILLARS ON WHITE OAK

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ABSTRACT. This study examined the seasonal pattern of leaf tie construction and occupancy by caterpillars associated with white oak, *Quercus alba*, in Missouri. Thirty white oak trees were monitored over the course of a season, recording the phenology of leaf tie construction, occupancy, and abandonment by 14 different species of leaf-tying caterpillars. Larvae of *Pseudotelphusa* sp. (Gelechiidae) created most of the initial leaf ties, many of which were secondarily occupied by a variety of other leaf tiers. In addition, non-tying caterpillar species from a variety of families were common secondary occupants. As many as 6 different species and 15 different individual larvae were found occupying a single leaf tie over the course of the season. In selecting pre-existing leaf ties for colonization sites, the leaf tiers did not discriminate between ties of different ages. On average, one-third of the leaves on a branch were incorporated into a leaf tie at some time during the season. Despite their abundance, leaf ties in this system appear to be a limiting resource.

Additional key words: Leaf tie, insect phenology, positive interactions, *Quercus alba*, shelter-builders.

Shelter-building caterpillars are a conspicuous component of the insect herbivore fauna attacking temperate broad-leaved trees (Frost 1959, Prentice 1965). A variety of caterpillars in at least 12 (Berenbaum 1999) and as many as 27 (Jones 1999) different families use silk to construct leaf ties, webs, folds, and rolls that typically serve as both shelters and feeding sites (room and board) for developing larvae. These leaf shelters are often colonized subsequently by other arthropods, including other shelter-building caterpillars (Carroll & Kearby 1978, Cappuccino 1993, Cappuccino & Martin 1994, Lill 1999, Martinsen et al. 2000, Lill & Marquis 2003), many of whom oviposit in existing shelters (Lill & Marquis 2004). In the case of leaf ties ("sandwiches" of overlapping leaves), there is often a high rate of secondary occupation by both leaf-tying and non-leaf-tying caterpillars (Carroll et al. 1979, Fukui 2001) resulting in multiple individuals of the same or different species co-occurring within a leaf tie. Such secondary occupation suggests that these shelters represent a potentially limiting resource for populations of leaf tiers and leaf tie associates and may, in part, influence the local abundance of caterpillars occupying individual host plants.

An important first step in understanding the dynamics of these interactions is to document the seasonal pattern of shelter construction (i.e., resource availability), maintenance, and occupancy (resource use) by different species of caterpillars. Here, I describe the natural history of leaf tie construction and occupancy of the leaf ties found on saplings of white oak (*Quercus alba* L.).

MATERIALS AND METHODS

This study was conducted in east-central Missouri at Cuivre River State Park. The park consists of second growth oak-hickory forest dominated by a canopy of white oak (*Q. alba*), black oak (*Q. velutina* Lam.), and hickory (*Carya* spp.) with an understory of flowering dogwood (*Cornus florida* L.), sassafras (*Sassafras albidum* Nees), redbud (*Cercis canadensis* L.), sugar maple (*Acer saccharum* Marsh) and various oak saplings. The study was conducted within the Big Sugar Creek watershed, an unmanaged natural area of the park.

Thirty small white oak trees (understory saplings) were tagged in early spring of 1996, prior to budbreak. Trees ranged in height from 2 to 4 m and had at least four accessible branches randomly assigned to one of two treatments, control and census (two branches each per tree). Leaf ties formed on census branches were opened regularly to record the occupants whereas leaf ties on control branches were left undisturbed. The to-

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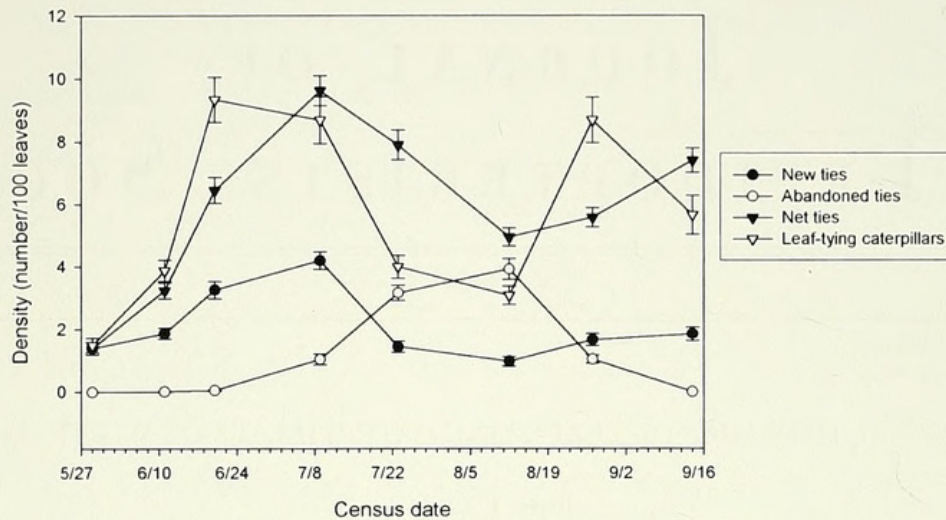


FIG. 1. Seasonal pattern of natural leaf tie formation and leaf-tying caterpillar density on white oak. Error bars are 1 SE.

tal number of leaves on each branch was recorded following budbreak. On 29 May, I established three permanent artificial leaf ties on one control and one census branch of each tree by clipping together haphazardly selected clusters of three adjacent leaves with lightweight curler clips (one clip/three-leaf cluster; Brentwood Beauty Labs International, Hillside, Illinois). Artificial leaf ties were created to sample the community of secondary occupants in a standardized manner (all artificial ties were initially unoccupied and established on the same date). Beginning 29 May, the number of all naturally occurring leaf ties present on each branch during eight census periods (29 May, 11 June, 20 June, 9 July, 23 July, 12 August, 27 August, and 14 September) was recorded. In addition, for all branches in the census treatment, the contents of the leaf ties (both natural and artificial) were recorded by briefly opening the ties and then clipping them back together with a curler clip. Any caterpillars that escaped from the ties by spinning down on silk were placed back into the leaf tie. The number and species of all leaf-tying caterpillars and non-tying associates (e.g., herbivorous beetles and non-tying caterpillars) were recorded during each census. Each leaf tie in the census treatment was assigned a unique label so the sequence of occupancy (for individual ties) could be followed. Clips were removed at subsequent censuses from any natural leaf ties that were not actively maintained (i.e., that came apart upon removal of the clip or that contained no leaf-tying caterpillars during two consecutive censuses). None of the leaf ties on control branches were opened, but the artificial ties on these branches were externally inspected for signs of occupancy (e.g., skeletonization damage, visible silk strands) to determine the timing of colonization.

The minimum number of total individuals and species of leaf-chewing insects (caterpillars, beetles, and sawfly larvae) occupying a leaf tie over its "life-span" was determined by examining the sequence of occupation of each natural leaf tie; consecutive records of the same species were always assumed to be a single individual, so these estimates were likely to be conservative. The relationship between the age of the leaf tie (expressed as the number of censuses in which it was maintained) and the total minimum number of species and individuals was examined with linear regression. In addition, for leaf ties maintained for a given number of censuses (3, 4, or 5), the effect of the date of tie origination on the total minimum number of species and individuals was examined graphically.

Because the attractiveness of leaf ties to potential colonists might be expected to change as a tie ages (accumulating damage, frass, and silk), I examined the influence of tie age on the likelihood of secondary colonization by leaf-tying caterpillars. The distribution of "new" colonization events (occupancy by one or more individuals of a species not present in the previous census) across natural ties of different ages was compared with a null distribution using a Chi-square test. The null distribution assumed that ties of different ages would be colonized in proportion to their relative availability (i.e., colonists would not discriminate among ties of different ages). Because late season colonists had the widest range of tie ages available to "choose" from, only the new colonization events that occurred during each of the last two censuses were considered in this analysis.

RESULTS

Leaf ties. The total abundance of naturally occurring leaf ties (census + control treatments) ranged from a

TABLE 1. Leaf-tying caterpillars colonizing white oak trees.

Family and species ^a	Peak density (larvae/100 lvs.)
Gelechiidae	
<i>Arogalea cristifasciella</i> Chambers	0.30
<i>Chionodes fuscomaculella</i> Chambers	0.30
<i>Pseudotelphusa</i> sp. (undescribed)	7.45
<i>Coleotechnites quercivorella</i> Chambers	0.01
Noctuidae	
<i>Morrisonia confusa</i> Hubner	0.06
Oecophoridae	
<i>Antaeotricha humilis</i> Zeller	0.03
<i>Antaeotricha osseella</i> Williamson	0.01
<i>Antaeotricha schlaegeri</i> Zeller	0.17
<i>Psilocorsis quercicella</i> Chambers	1.86
<i>Psilocorsis cryptolechiella</i> Chambers	2.64 ^b
<i>Psilocorsis reflexella</i> Clemens	—
<i>Setiostoma xanthobasis</i> Zeller	0.04
Pyrallidae	
<i>Tetralopha expandens</i> Walker	0.23
Tortricidae	
<i>Anclis divisana</i> Walker	0.07

^a Nomenclature and authors follow Hodges (1983).

^b Density data for *P. cryptolechiella* and *P. reflexella* are combined because early instars of these two species could not be distinguished.

low of 154 on 29 May (census 1) to a high of 1265 on 9 July (census 4). However, because branches varied in size (mean \pm 1 SE = 107.6 \pm 6.0 leaves), tie densities (no. leaf ties/leaf) were used in all analyses. Census branches and control branches did not differ from each other in the mean density of leaf ties in any of the eight censuses ($p > 0.10$ for all paired *t*-tests), suggesting that the disturbance and use of clips in the census treatment did not adversely affect tie formation patterns.

The rate of leaf tie formation (mean number of new leaf ties per census branch) increased markedly between mid- and late June and peaked in early July during which time an average of four new leaf ties were formed per 100 leaves on each of the 60 census branches (Fig. 1). Following this peak, the rate of tie formation declined markedly while the number of abandoned ties (those that were empty and/or not maintained) increased, resulting in a decline in the net number of leaf ties present on the branches. During the last two censuses (late August and mid-September), the rate of new tie formation increased slightly while the number of abandoned old ties declined rapidly, resulting in a second peak in net tie density.

The total density (accumulated over the season) of natural leaf ties formed on a branch in the census treatment varied from 6.4 to 34.6 ties/100 leaves (mean \pm 1 SE = 17.6 \pm 0.80). Since most leaf ties consisted of two leaves, this means that on average, slightly more than one-third (17.6 \pm 2 = 35.2/100) of the leaves on a given branch were incorporated into a leaf tie at some point during the season. Because nat-

ural leaf ties on the control branches were not followed individually, their seasonal pattern of tie formation, occupancy, and abandonment could not be examined. The total density of natural leaf ties formed on a census branch over the course of the study was positively related to the density of initial leaf ties formed early in the season (i.e., by the second census on June 11; $r^2 = 0.16$, $F_{1,58} = 10.89$, $p = 0.002$).

Occupants. Over the course of the season, 14 different species of leaf-tying caterpillars (Table 1) were recorded as occupants of the naturally occurring leaf ties ($N = 1162$) on the census branches. Across the season, the density of leaf-tying caterpillars (all 14 species combined) varied from a low of 1.49 to a high of 9.50 larvae/100 leaves (Fig. 1). The density of leaf tiers peaked in late June and again in late August, slightly in advance of the peaks in leaf tie density. Among the seven most common species of leaf tiers, *Pseudotelphusa* sp. (Gelechiidae, currently unnamed) achieved the highest peak density (Table 1), and its two population peaks (representing its two generations) preceded the peaks of the other bivoltine species (Fig. 2). Three species of Oecophoridae in the genus *Psilocorsis* (*P. cryptolechiella*, *P. quercicella*, and *P. reflexella*) were the next most prevalent, with peak densities >1 per 100 leaves.

Individual leaf ties varied considerably in the number of species of leaf tiers colonizing them, ranging from a low of zero (for ties that had been created and abandoned prior to a census) to as many as six different species occurring in a single tie over its lifespan. The total number of individuals occupying a leaf tie over its lifespan varied from 0–15 (mean \pm 1 SE = 2.33 \pm 0.06). Within a particular census, it was not uncommon to find assemblages of several individuals from 2–3 different species sharing a leaf tie (the record was 9 caterpillars of 3 different species).

Leaf ties that hosted both a greater abundance and higher species richness of caterpillars were maintained for longer periods (Fig. 3). However, most ties were relatively ephemeral, lasting on average 3.3 \pm 0.1 censuses (a little more than a month). Of 91 natural ties recorded on census branches during the first census, only 10 (11%) persisted until the last census. However, for those natural ties ($N = 302$) formed during the first peak of leaf tie construction (9 July, census 4), almost a third (27%) were still occupied on the last census (14 September), which was near the second peak in leaf tie construction (see Fig. 1). The date that a leaf tie was formed also influenced the total abundance and species richness of colonists. For leaf ties that persisted for an equal number of censuses (either 3, 4, or 5), the average abundance and species richness tended

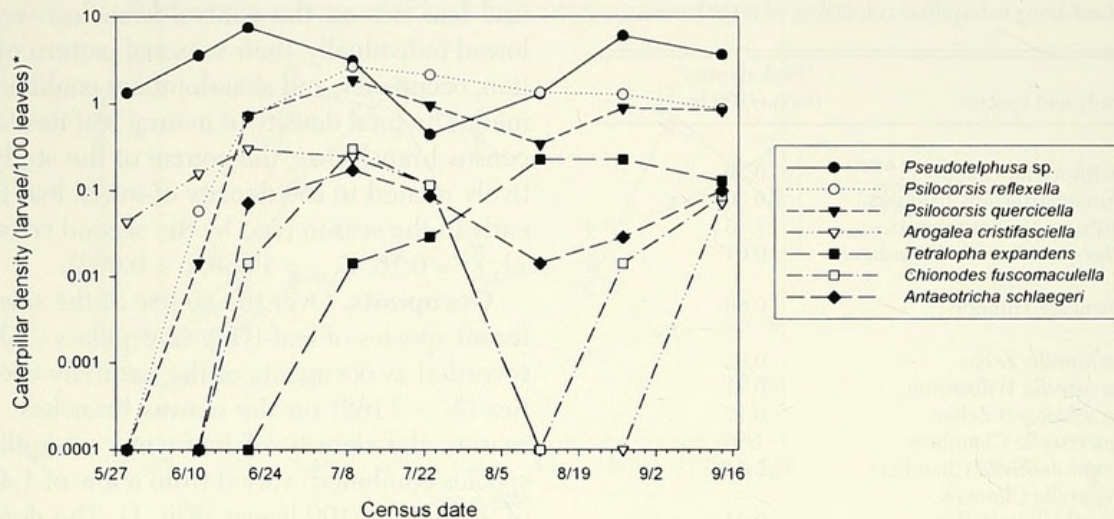


FIG. 2. Seasonal dynamics of seven species of leaf-tying caterpillars on white oak. New ties are ties that had not been recorded in a previous census; abandoned ties were not maintained and came apart readily upon examination; net ties = ties present in the previous census + new ties – abandoned ties. Note log scale of ordinate.

to increase with later date of origination (Fig. 4), suggesting that new ties formed later in the season are subject to higher levels of secondary colonization than those formed earlier.

As the season progressed, heavily utilized leaf ties became highly damaged and accumulated frass from previous occupants, decreasing the amount of food available for developing larvae. Despite this apparent decline in resource quality, the age of the leaf tie had no influence on the probability of colonization by leaf tying caterpillars late in the season. For old ties (ties that had been established at least one census prior), the probability of a new colonization event was unrelated to tie age (i.e., the observed distribution of colo-

nization events across ties of different ages was not different from the null expectation in either of the last 2 censuses; census 7: $\chi^2_{1,5} = 3.49$, $p > 0.50$, $N = 299$; census 8: $\chi^2_{1,5} = 9.17$, $p > 0.10$, $N = 119$).

An additional 342 non-tying individuals, including 12 species of Lepidoptera, two leaf-feeding beetles, and one sawfly larva, were also found inhabiting the ties (Table 2). Non-herbivorous inhabitants were not recorded, but included click beetles, psocids, rove beetle adults and larvae, shield bugs, thrips, and lacewing larvae. Spiders often occupied the ties as well, occasionally making nests (with egg masses) inside the ties.

Artificial ties. Artificial ties were readily colonized both by leaf-tying caterpillars and by non-tier associates. By late June, ninety-five percent of the 180 artificial leaf ties had been colonized by leaf tiers and all remaining ties were colonized by late July. For the 90 artificial tier ties on the census branches, a total of 733 leaf tier caterpillars and 202 non-tier associates were recorded during the seven censuses. All leaf tier species listed in Table 1 except *Anclis divisana* and *Tetralopha expandens* colonized the artificial ties. The density of leaf-tying caterpillars occupying these artificial leaf ties was similar to that observed for the natural ties.

DISCUSSION

There was marked seasonal variation in the construction of new leaf ties. Because *Pseudotelphusa* sp. larvae were the first leaf tiers to appear, they were largely responsible for the initial wave of ties, which were subsequently colonized by the later-appearing species (Fig. 2). The increased densities

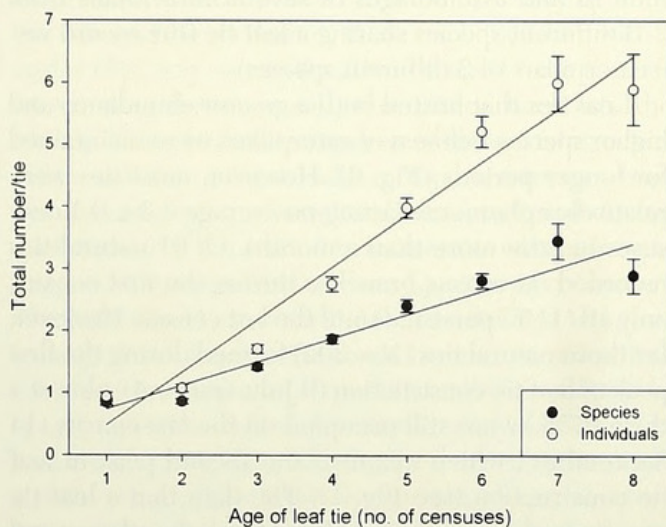


FIG. 3. Total number of individuals and species of leaf-chewing insects recorded in leaf ties maintained for variable lengths of time. Each data point is a mean of a different set of leaf ties (data are not cumulative).

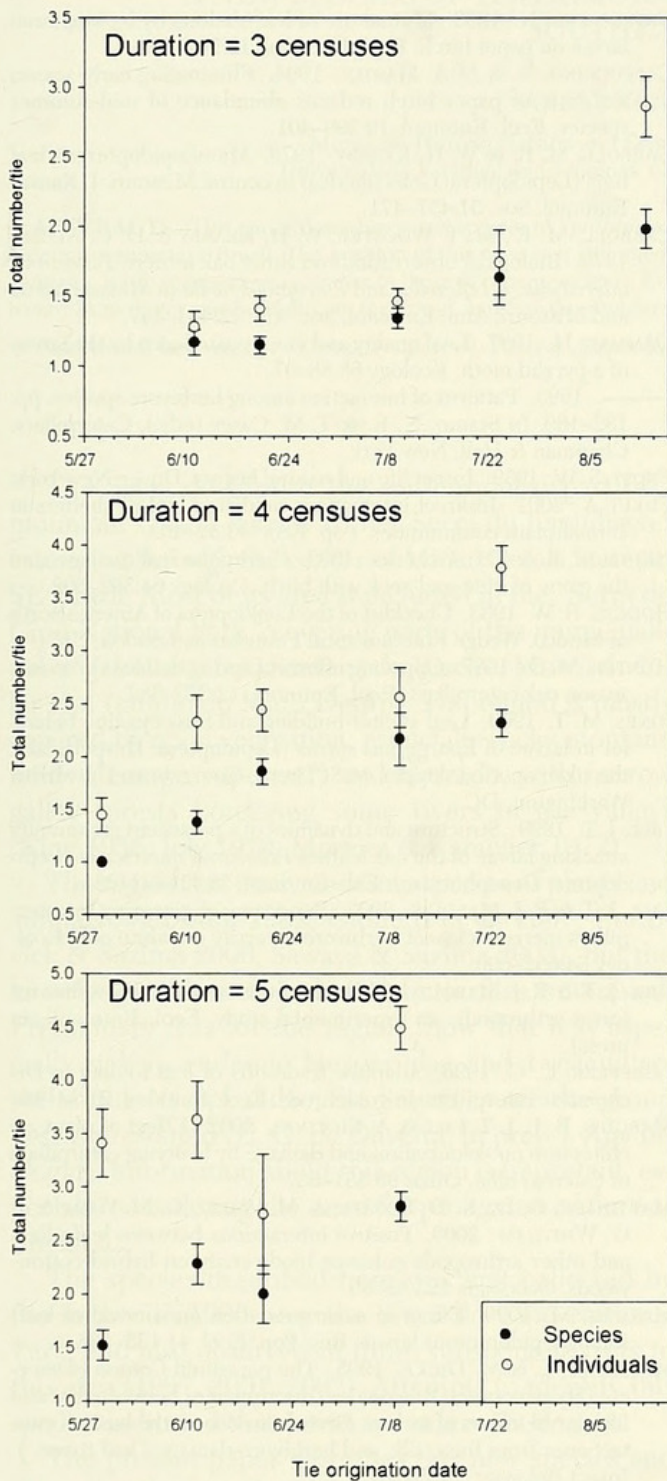


FIG. 4. Total number of individuals and species of leaf-chewing insects recorded in leaf ties originating on different dates, but maintained for equal periods of time (3–5 censuses). Error bars are 1 SE.

of leaf tiers relative to leaf ties during the early season (Fig. 1) could be explained by the fact that most of these early leaf ties were created by small groups (2–3) of *Pseudotelphusa* sp. larvae. The lack of a second peak in the production of new leaf ties during the late season (i.e., when leaf-tying caterpillar abundance reached its second peak) indicated that many of the new colonists (including the second wave of

TABLE 2. Non-leaf-tying herbivores (leaf-chewers) found inside leaf ties.

Order	Family	Species*
Coleoptera	Chrysomelidae	<i>Pachybrachis</i> sp.
	Curculionidae	<i>Cyrtopistomes castaneus</i> Roelfs
Hymenoptera	Tenthredinidae	<i>Caliroa</i> sp.
Lepidoptera	Arctiidae	<i>Halysidota tessellaris</i> JE Smith
	Bucculatricidae	<i>Bucculatrix</i> nr. <i>albertiella</i>
	Gelechiidae	<i>Trypanisma prudens</i> Clemens
	Limacodidae	<i>Isa textula</i> Harris
		<i>Parasa indetermina</i> Bdv
		<i>Sabine stimulea</i> Clemens
	Lymantriidae	<i>Dasychira obliquata</i> Grt. & Rob.
	Noctuidae	<i>Acrionicta increta</i> Morr. <i>Meganola miniscula</i> Zeller
	Notodontidae	<i>Lochmaeus manteo</i> Doubleday <i>Natada gibbosa</i> JE Smith
	Oecophoridae	<i>Machimia tentoriferella</i> Clemens

* Nomenclature and authors of Lepidoptera follow Hodges (1983).

Pseudotelphusa sp.) were preferentially occupying pre-existing ("old") leaf ties. Because most leaf ties were colonized and maintained by a succession of larvae of various species, the local density of leaf ties formed early in the season should have positively influenced the rate of colonization (and perhaps folivory) later in the season. The positive relationship between early season leaf tie density and the density of leaf ties formed over the entire season lent some support to this idea, but experimental studies are needed to separate innate host plant effects (some trees are simply more attractive to leaf tiers) from the domino effects arising from sequential occupancy of pre-existing ties.

The increase in abundance and species richness of insect herbivores with later date of leaf tie establishment (after controlling for tie age; Fig. 4) most likely reflected the seasonal increase in the size of the species pool of herbivores; more species were available to colonize a limited resource, resulting in more crowded leaf ties. There were a variety of late-season species not present earlier, whereas virtually all of the early summer species were also found in late summer, since most of these early species are bivoltine.

The rapid colonization of the artificial leaf ties by leaf tiers suggests that these species actively seek out pre-existing ties. Because many of these secondary occupants were early instar caterpillars, it appears that female moths are selecting pre-existing shelters as oviposition sites (wherein hatching larvae typically take up residence). Ovipositing in pre-existing shelters may provide several benefits to developing offspring, including a favorable microclimate that decreases the risk of dessication, decreased construction costs (in

terms of both time and energy), and decreased apparency to visually foraging predators (Fukui 2001). There are also potential costs to occupying pre-existing shelters, most of which are related to the negative effects of direct and indirect competition (Damman 1993). For example, pre-existing shelters are often highly damaged, contain large amounts of frass, and are often occupied by other caterpillars, all of which have been shown to increase the risk of predation by members of the third trophic level (Heinrich & Collins 1983, Steiner 1984, Mattiacci & Dicke 1995, Masashi 1999, Weiss 2003).

In addition, the surfaces of many "old" leaf ties have been skeletonized by previous occupants and would appear to offer little food resources to new colonists. However, because early instar caterpillars have relatively modest food requirements and later instars can add leaves to their natal shelter or create new shelters, it is quite possible that future food limitation has little bearing on adult oviposition decisions in this system. In this study, caterpillars colonized leaf ties of different ages in proportion to their relative abundance on the study trees, suggesting that ovipositing moths are not particularly selective about the age of leaf ties chosen for oviposition sites. Previous studies have shown that shelter-building caterpillars often choose leaves that promote effective and efficient shelter construction, even at the expense of food quality (Damman 1987, Hunter 1987, Reavey 1991, Loeffler 1996).

The diversity of ways in which caterpillars engineer their environment through the production of leaf shelters is only just beginning to be explored. More studies that investigate the costs and benefits of shelter-building as a putative adaptive trait are needed, as are studies that examine the ecological consequences of the behavior for plants and the communities of arthropods that associate with them. In addition, our understanding of the natural history of these small, inconspicuous, yet often abundant caterpillars is extremely limited; collecting and rearing efforts are needed to improve morphological descriptions and determine the host plant affinities and life histories of many of these poorly-known shelter-builders.

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