Leaf Pubescence Affects Distribution and Abundance of Generalist Slug Caterpillars (Lepidoptera: Limacodidae)

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ABSTRACT Insect herbivores often respond to leaf texture in making oviposition or feeding choices. This study examined the importance of leaf pubescence for an assemblage of generalist caterpillars (Lepidoptera: Limacodidae) feeding on oaks (*Quercus* spp.) and a variety of other tree species in eastern North America. Based on 10 yr of larval sampling on canopy and understory black and white oak (*Quercus velutina* and *Q. alba*, respectively) in the Ozark Mountains of Missouri, larval density of slug caterpillars (14 species as a group and 3 individual species) was higher on glabrous canopy leaves of *Q. velutina* than on highly pubescent understory leaves of that species. In contrast, there was no effect of stratum on overall density for *Q. alba*, which has glabrous leaves in both microenvironments. Individually, stratum effects for *Q. alba* were significant for five species, four of which were more abundant in the understory. Additional censusing of larvae on 20 tree species varying in leaf pubescence found that, as a group, slug caterpillar density was negatively correlated with leaf hair density. Finally, feeding trials confirmed that slug caterpillars prefer canopy over understory leaves of *Q. velutina* and vice versa for *Q. alba* leaves. When hairs were experimentally removed from one side of *Q. velutina* understory leaves, caterpillars preferred the side from which hairs were removed over the intact side. Together, these results indicate that leaf pubescence influences patterns of host plant use by these generalist herbivores, and in so doing, contributes to the structuring of local herbivore communities.

KEY WORDS canopy, Limacodidae, Missouri, oak, trichome

Leaf trichomes influence patterns of insect herbivory and insect abundance for a variety of plant species (reviewed in Levin 1973, Johnson 1975, Southwood 1986). Pubescence traits can mediate various aspects of the plant–herbivore interaction, including herbivore attraction to the host plant (Southwood 1986), adult attachment and/or oviposition (Callahan 1957, Webster et al. 1975, Roberts et al. 1979, Robinson et al. 1980, Gannon et al. 1994, Haddad and Hicks 2000, Malakar and Tingey 2000), egg survival (Poos and Smith 1931, Schillinger and Gallun 1968), insect growth (Lambert et al. 1992, Malakar and Tingey 2000), insect movement (Webster et al. 1975, Eisner et al. 1998, Zvereva et al. 1998), insect survival (Gilbert 1971, Eisner et al. 1998, Haddad and Hicks 2000), and pupal mass (Malakar and Tingey 2000). However, far from being a general defense, the effect of pubescence may be positive, negative, or nonexistent, depending on the particular herbivore species (Southwood 1986, Hare and Elle 2002) and the leaf hair type (glandular or nonglandular), density, and length (Andres and Connor 2003). In general, long-legged probing and sucking insects (e.g., Hemiptera) tend to be less deterred by trichomes, whereas species with a high degree of ventral contact with leaf surfaces (e.g., many lepidopteran and sawfly larvae) seem to be more easily deterred (Levin 1973, Southwood 1986, Hare and Elle 2002). For many small chewing insects, a dense mat of leaf hairs can present a formidable barrier to leaf feeding, requiring extensive grazing before the leaf blade can be accessed (Malcolm 1995), whereas for other insects, leaf hairs serve as an ideal structure with which to cement eggs and are preferred oviposition sites (Lambert et al. 1992). The world in which these pubescence-sensitive insect herbivores must maneuver is a complex one: the expression of foliar pubescence can be influenced by genotype, the abiotic environment, leaf developmental stage, and previous folivory (Ehrlinger et al. 1976, Southwood 1986, Baur et al. 1991, Ågren and Schemske 1994, Agrawal 1999, Roy et al. 1999, Kärkkäinen and Ågren 2002, Zalucki et al. 2002).

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While much attention has been given to chemical defense in structuring herbivore communities (Berenbaum 1981, Jones and Lawton 1991, Dungey et al. 2000), the role of morphological defenses has been relatively less characterized (but see Gomez et al. 1986, Ezcurra et al. 1987, Fritz et al. 1994, van Dam and Hare 1998, Andres and Connor 2003). Although numerous studies have examined species-specific responses of insect herbivores to leaf pubescence traits, very few ecological studies have examined the responses of entire communities, guilds, or assemblages, particularly in nonagricultural systems (but see Ezcurra et al. 1987 and Andres and Connor 2003). The two studies that have examined community-level responses to pubescence traits in detail produced somewhat differing results. In manzanitas (*Actostaphylos* spp.), all feeding guilds except leaf miners were lower in abundance on species with longer trichomes, whereas the abundance of external folivores responded positively to trichome density and glandularity (Andres and Connor 2003). On madrone (*Arbutus xalapensis*), Ezcurra et al. (1987) found that pubescence deterred feeding by some guilds (gall formers, external chewers, and leaf miners), but had positive effects on sucking insects, in contrast to the patterns found in manzanitas. The current study examines the role of pubescence in determining the spatial distribution of an assemblage of generalist tree-feeding herbivores, the slug caterpillars (Lepidoptera: Limacodidae), feeding on a variety of host tree species varying in foliar pubescence.

Within the Lepidoptera, the family Limacodidae is part of a monophyletic clade in the superfamily Zygaenoidea, which also includes the families Aididae, Dalceridae, Megalopygidae, and Somabrachyidae (known as the "limacodid group" families; Epstein 1996). Caterpillars in the family Limacodidae are noted for their colorful and sometimes elaborate morphologies, which can include aposematic coloration, stinging setae, and an array of dorsal protrusions (e.g., warts, scoli, and tubercles) of various kinds (Dyar and Morton 1895, Epstein 1996, Wagner 2005). They derive their common name, slug caterpillars, from their locomotory habit, characterized by a high degree of ventral contact with the substrate, the use of abdominal "sucker" appendages in movement (in place of prolegs), and the secretion of semifluid silk and/or associated fluids that serve to enhance substrate contact (Epstein 1995). Some limacodids are important economic pests on tropical palms (Holloway 1987, Holloway et al. 1987, Godfray and Chan 1990, Conant et al. 2002) and on temperate deciduous trees (Heitzman and Heitzman 1987). Within eastern North America, slug caterpillars occur mainly late in the growing season (peaking in August and September) and feed almost exclusively on old foliage of various woody plants (Wagner 2005).

Despite their wide distributions in both temperate and tropical regions, slug caterpillars rarely have been the focus of formal ecological study. This lack of study may stem from the fact that, in many locations, the densities of limacodids are generally low, based on their relative frequencies in a variety of general caterpillar collections/surveys (Basset 1999, Barbosa et al. 2001). Despite these low abundances, three general ecological observations regarding limacodid larvae have been reported: (1) they tend to be rather polyphagous in both temperate and tropical areas (Godfray et al. 1987, Epstein 1996, Wagner 2005); (2) they show an apparent preference (although unquantified) for smooth-leaved plants (Dyar 1899b, Covell 1984, Godfray et al. 1987, Epstein 1988, 1995, Wagner 2005); and (3) a number of species are reported to occur most commonly on low-hanging, understory foliage (Dyar 1896a, 1897c). Epstein (1988) subsequently linked the first two observations by suggesting that slug caterpillars are adapted to be leaf texture specialists, avoiding species with pubescent leaves but otherwise paying little heed to plant chemistry or plant phylogeny (the "glabrous host hypothesis"). He also suggested the characteristic late-season appearance of limacodid larvae (which are typically found only in the late summer and fall in the temperate zone) may have resulted from natural selection to avoid early season leaves, which tend to have some transitory pubescence, even in species whose leaves are otherwise glabrous for the majority of their life (e.g., *Quercus alba*). Previous work on an Asian palm-feeding limacodid (*Setora* sp.) found a negative correlation between trichome density on coconut leaves and caterpillar density (Soekarjoto et al. 1979, Taulu et al. 1980), suggesting that trichomes present a partial barrier to establishment of early instars (Godfray et al. 1987). Apart from these data, however, the hypothesis that limacodid larvae prefer smooth-leaved hosts remains unexamined.

We tested Epstein's glabrous host hypothesis in three ways. First, we used long-term census data to compare the natural densities of limacodid larvae between strata (canopy versus understory) of two common host plant species with contrasting patterns of leaf pubescence. In the shaded understory, leaf laminae of *Quercus velutina* (black oak) are hairy, especially on the lower surface, whereas canopy *Q. velutina* (e.g., sun leaves) lack noticeable pubescence and are highly glabrous, smaller, and more deeply lobed. In contrast, there is relatively little difference in pubescence in *Quercus alba* (white oak) leaves from different strata (they are all glabrous), although canopy leaves are smaller and more deeply lobed. If Epstein's hypothesis is correct, limacodids should occur in higher densities on canopy leaves than on understory leaves of *Q. velutina* but should show no differences between leaf types in *Q. alba*, all other factors being equal. Second, in 1999 and 2000 we sampled understory plants of 18 woody species (in addition to *Q. velutina* and *Q. alba*), recording the density of slug caterpillars and quantifying leaf pubescence. We predicted that slug caterpillar density would be a decreasing function of the mean density of leaf hairs. In addition, because most caterpillars are found on the lower surface of leaves (Marquis and Passoa 1989), we predicted caterpillar density would be most strongly correlated with pubescence found on the underside of

leaves of each plant species. Third, we conducted feeding trials to separate the effects of pubescence from other ecological factors known to vary between strata and among plant species.

Materials and Methods

Field Sampling. We visually censused caterpillars on permanently marked black and white oak trees (*Q. velutina* Lam. and *Q. alba* L., respectively) in the Ozark Mountains of southeast Missouri from 1993 to 2004. Censusing was conducted as part of the Missouri Ozark Forest Ecosystem Project (MOFEP), a long-term study examining the effects of three forest management treatments (control, selective logging, and clear-cutting) on landscape-level biodiversity (Brookshire and Shifley 1997). All limacodids found on marked trees or branches that could be field identified were recorded without removal. Unknown limacodids were collected and reared in the laboratory and identified as adults. Caterpillar censuses were conducted four times per season (beginning early May, mid-June, mid-July, and late-August/early September) in both the understory (1993–2004) and the canopy (1994–2004). Although limacodid larvae were occasionally recorded in the July census in some years, these were typically early instars, which were difficult to identify definitively to species and/or which were likely to have been rerecorded in the last census, because of their long development times. Because of this and the fact that, in every year, the vast majority (>95%) of limacodid records were found only during the last census, only data from the annual August censuses are presented here. The application of the forest management treatments in 1996 prevented any data collection in that year (for either stratum). While caterpillar density varied significantly among years, landscape-level treatment effects were comparatively small when detected (Forkner et al. 2006), and as a result, are not considered further (data from the different treatments are pooled in all analyses). In the understory, in excess of 800 trees (both tree species combined) in 54 stands spread over three counties were sampled each year (368.8 ± 11.7 and 769.9 ± 39.9 m^2 of foliage/yr [SE] summed across all stands for *Q. velutina* and *Q. alba*, respectively). Understory stands consisted of small clusters of saplings and ground accessible branches of subcanopy to canopy trees initially containing 3,000 (*Q. alba*) and 1,200 (*Q. velutina*) leaves spread among at least five individuals per species. All 54 understory stands contained *Q. alba*, whereas only 43 contained both *Q. alba* and *Q. velutina.* Canopy censusing was conducted using a bucket truck that enabled access to upper canopy leaves. Canopy sampling consisted of three trees per oak species in each of 12 stands (72 trees total, 108.1 ± 4.7 and 122.1 ± 5.1 m^2 foliage/yr for *Q. velutina* and *Q. alba*, respectively). For further details of the sampling and maps of the study sites, refer to Brookshire and Shifley (1997) and Forkner et al. (2006).

For each year, the density of all limacodid caterpillars found on each oak species and in each stratum was computed by dividing abundance (summed across all trees) by total leaf area sampled. Leaf area sampled was estimated as the product of total leaf number (counted in June of each year for all sampled trees or branches) and mean leaf area per leaf type (canopy black oak = 63.5 ± 21.4 cm^2, understory black oak = 96.7 ± 59.3 cm^2, canopy white oak = 52.1 ± 21.4 cm^2, understory white oak = 58.7 ± 28.5 cm^2; $N = 200$ leaves per species and stratum combination). Total limacodid density (all species combined) was log-transformed and analyzed with paired *t*-tests (Zar 1999), comparing annual canopy and understory densities on each oak species. Because all analyses were based on densities (larvae per meter squared of foliage), we were able to control for differences in the sampling effort between canopy and understory. Because density data for individual caterpillar species were heteroscadistic and could not be satisfactorily transformed to meet assumption of parametric tests, we used Wilcoxon's paired sample tests (Zar 1999) to compare the canopy and understory rank densities (also for each oak species separately). This test is the nonparametric equivalent of a paired *t*-test, with the ranks from each stratum paired by sampling year. In both the combined and individual species analyses, the 10 years of data containing both canopy and understory samples (1994, 1995, 1997–2004) were used as paired replicates. Because the Wilcoxon paired sample test ignores years for which both strata have zero values (Zar 1999), single species comparisons among strata were restricted to the most common species (species with six or more pairs of years with at least one nonzero density value).

In an additional test of the effects of pubescence on the abundance of limacodid caterpillars, we censused 20 woody plant species (from an array of plant families, and including *Q. alba* and *Q. velutina;* Table 1) that vary in leaf pubescence for understory-grown individuals. Limacodidae have been recorded by us to feed on each of these plants species or are recorded in the literature to do so (Dyar and Morton 1895, Dyar 1896–1899, Wagner 2005). These species spanned a range of mean pubescence, from entirely glabrous (e.g., *Prunus serotina*, *Cercis canadensis*, and *Quercus alba*) to densely hairy (e.g., *Cornus florida*, *Fraxinus americana*, and *Quercus imbricaria;* Table 1). Specifically, in a 9-ha tract of forest (6 km West of Krakow, MO: 38°28′22″ N, 91°06′06″ W), between 9 and 13 individuals per plant species were surveyed for all insect herbivores in late August/early September 1999 and 2000. The site (Whiskey Creek Sheep Farm) was selectively logged 35 yr ago. We recorded all insect herbivores encountered in searching top and bottom of all leaves. The total number of limacodid caterpillars encountered (all species combined) was expressed as the number encountered per square meter of leaf area. Average leaf area surveyed (16.8 m^2 per species across all species; Table 1) was estimated as above for each tree species separately. Pubescence was quantified by counting the number of hairs on one spot (3 mm diameter, approximately halfway along the length of the leaf and halfway between the midrib and

Table 1. Densities of larval Limacodidae recorded on pubescent and nonpubescent host tree species in eastcentral Missouri

Plant species (family)	No. trees censused	Total leaf area censused (m^2)	Leaf pubescence (no. hairs per $mm^2 \pm SE$ on the lower/upper leaf surface)	Total density (larvae per m^2)
Acer saccharum Marsh. (Aceraceae)	10	24.5	0.4 ± 0.2/0.0 ± 0.0	0.20
Bumelia lanuginosa (Michaux) Pers. (Sapotaceae)	8	0.9	3.0 ± 0.3/0.1 ± 0.1	0.00
Carya cordiformis (Wang.) K. Koch. (Juglandaceae)	13	15.1	3.9 ± 0.6/0.8 ± 0.2	0.07
Carya ovata (Mill.) K. Koch. (Juglandaceae)	10	19.5	1.9 ± 0.3/0.0 ± 0.0	0.15
Celtis occidentalis L. (Ulmaceae)	11	8.6	1.9 ± 0.2/0.7 ± 0.1	0.93
Cercis canadensis L. (Caesalpinaceae)	12	18.3	0.0 ± 0.0/0.0 ± 0.0	1.92
Cornus florida L. (Cornaceae)	13	26.6	6.1 ± 0.6/5.8 ± 0.5	0.04
Diospyros virginiana L. (Ebenaceae)	10	10.8	1.4 ± 0.4/0.5 ± 0.1	0.00
Fraxinus americana L. (Oleaceae)	11	13.4	6.2 ± 0.5/0.0 ± 0.0	0.00
Juglans nigra L. (Juglandaceae)	10	12.7	2.7 ± 0.2/0.0 ± 0.0	0.00
Prunus serotina Ehrh. (Rosaceae)	11	9.5	0.0 ± 0.0/0.0 ± 0.0	1.47
Quercus alba L. (Fagaceae)[a]	10	38.0	0.0 ± 0.0/0.0 ± 0.0	0.97
Quercus imbricaria Michx. (Fagaceae)	9	6.4	5.6 ± 0.6/0.0 ± 0.0	1.09
Quercus rubra L. (Fagaceae)	10	20.5	0.0 ± 0.0/0.1 ± 0.1	0.34
Quercus stellata Wang. (Fagaceae)	9	18.7	2.1 ± 0.3/0.9 ± 0.3	0.32
Quercus velutina Lam. (Fagaceae)[a]	12	24.4	3.0 ± 0.6/1.0 ± 0.2	0.37
Sassafras albidum (Nutt.) Nees (Lauraceae)	11	15.0	0.5 ± 0.4/0.1 ± 0.1	0.00
Ulmus rubra Muhl. (Ulmaceae)	12	13.4	2.5 ± 0.3/1.4 ± 0.2	0.00
Viburnum rufidulum Raf. (Caprifoliaceae)	12	8.0	0.0 ± 0.0/0.0 ± 0.0	0.37
Zanthoxylum americanum Miller (Rutaceae)	10	12.6	4.1 ± 0.7/0.4 ± 0.2	0.00

[a] These host plant species were sampled in each of 2 yr (1999 and 2000), whereas all other host plants were sampled in only 1 of the 2 yr. For these two species, the abundance and leaf area sampled were summed across the 2 yr to calculate density.

leaf edge) on each of the lower and upper surfaces of the leaf, two leaves per plant, and five plants per plant species. Leaves were collected in September to coincide with the time of highest slug caterpillar abundance and so that our estimates of trichome density would not be affected by differences in leaf expansion (all leaves first appeared in April–May of that year). Differences in caterpillar abundance related to density of leaf hairs (mean of the five plants per species) were tested with Spearman rank correlations (lower and upper surfaces tested separately; Zar 1999). Low densities of larvae in the 2 yr of sampling precluded analyses of host plant preferences of individual species.

Laboratory Feeding Trials. As a further test of the role of leaf pubescence in determining distribution patterns, we performed two feeding trials in the laboratory in the summer of 2005. In the first trial, we compared foraging and feeding on leaves from canopy (glabrous) versus understory (pubescent) leaves of *Q. velutina*, and between leaves of *Q. alba* from these two strata (both glabrous). Mean number of hairs per square millimeter (±SE) on the bottom and top of *Q. velutina* understory leaves were 2.3 ± 0.1 and 1.0 ± 0.1, respectively. Both sides of canopy leaves of *Q. velutina* and *Q. alba*, as well as understory *Q. alba*, were completely glabrous. All leaves were collected at the Tyson Research Center, Eureka, MO (owned and operated by Washington University). Access to canopy leaves was through a boom truck. On 1 September 2005, numerous twigs with three to six attached leaves representing each tree species and stratum combination were collected, the twig was placed immediately in an aquapic filled with water, and the aquapic and leaves were covered by a 940-ml plastic container to reduce transpiration. They were then transported to the laboratory, where on 2 September 2005, choice arenas were set up, consisting of a canopy leaf and an understory leaf of the same tree species ($N = 30$ per tree species). The leaves remained attached to their twig (all others had been trimmed away); twigs remained in water-filled aquapics. The two leaves, matched for approximate area, were clipped together with hair clips, top side to top side, to force caterpillars to forage on the undersides of the leaves. At the start of the trial, a single caterpillar per leaf pair was placed on the two leaf petioles, and the entire setup, leaves upright, was re-enclosed by a 940-ml container. At 24 and 48 h, position of the caterpillars with respect to stratum was recorded. At 72 h, leaf area consumed was measured with a clear plastic grid to the nearest 1 mm^2. The following species of caterpillars were used, with numbers of individuals in parentheses: *Isa textula* (17), *Adoneta spinuloides* (16), *Natada nasoni* (14), *Lithacodes fasciola* (6), *Prolimacodes badia* (4), and *Euclea delphinii* (3). Caterpillars (fourth to sixth instars) were field-captured; therefore, the number of each in the experiment was determined by availability in the field. Total sample size was reduced to 24 and 23 for *Q. velutina* and *Q. alba*, respectively, because six and seven caterpillars were parasitized or pupated during the experiment. Differences in position across the 2 d were first tested with the nonparametric equivalent of a repeated measures and the Cochran-Mantel-Haenszel statistic for individual effects (Stokes et al. 1995), followed by a χ^2 test (Zar 1999). Differences in amount eaten after 72 h were tested with a Wilcoxon's paired sample test (Zar 1999). There was insufficient replication to examine the responses of individual species; therefore, the results reported below pertain to the entire assemblage, treating each larva as a replicate.

In the second feeding trial, caterpillars were placed on the midrib of an understory leaf of *Q. velutina*, from

Table 2. Descriptive statistics for species of Limacodidae recorded on black and white oak in southeast Missouri (1993–2004)

Species	*N*	CV[a]	Min[b]	Max[b]	Incidence[c]
Acharia stimulea	16	0.88	0	0.0027	8
Adoneta spinuloides	112	0.72	0	0.0161	9
Apoda biguttata	206	0.81	0.0020	0.0316	11
Euclea delphinii	104	0.89	0	0.0179	10
Isa textula	257	0.82	0.0008	0.0445	11
Isochaetes beutenmuelleri	82	2.22	0	0.0389	9
Monoleuca semifascia	2	—	0	0.0008	2
Natada nasoni	142	1.03	0.0016	0.0344	11
Packardia geminata	4	—	0	0.0008	4
Parasa chloris	32	1.04	0	0.0074	9
Parasa indetermina	13	1.04	0	0.0022	6
Phobetron pithecium	52	1.49	0	0.0169	8
Prolimacodes badia	57	1.13	0	0.0124	8
Tortricidia sp. group	244	0.70	0.0019	0.0409	11
Total[d]	1,348	0.65	0.0102	0.1994	

[a] Coefficient of annual variation (SD/Mean); CV was calculated using annual densities (individuals per meter squared leaf area) of each species summed across oak species and strata. Dashes indicate species whose densities were too low to compute a meaningful statistic.
[b] Minimum/max annual densities calculated as described in footnote a.
[c] The no. of years out of 11 that at least one individual was recorded.
[d] This total also includes 25 limacodid larvae that could not be positively identified to species in the field.

which the pubescence on a lateral half of the leaf had been gently rubbed off (without obviously wounding the plant), the other half of the leaf remaining intact ($N = 20$). The nonexperimental (pubescent portion) of the leaf was handled for a similar amount of time to control for potential "handling effects" on measured insect responses. Leaves had been collected the same day (30 September 2005), and otherwise prepared in feeding chambers as above. After 24 h, the position of the caterpillar on the leaf and amount of leaf area eaten were recorded. Caterpillars (last instars) had been field caught and were represented by the following species (numbers in parentheses): *I. textula* (11), *N. nasoni* (6), *L. fasciola* (1), *P. badia* (1), and *A. spinuloides* (1). Two caterpillars pupated during the experiment, reducing the sample size to 18 larvae. Experimental effects on position after 24 h and amount eaten were tested with a Fisher exact test (Zar 1999) and a one-tailed Wilcoxon paired sample test (Zar 1999), respectively, again treating each larva as a replicate. Because we were limited to using a mixture of locally available species in both sets of feeding trials, we view these tests as conservative, because individual species may show variable responses to pubescence, decreasing our ability to detect an "overall" effect of the combined set.

Results

Field Sampling. A total of 1,348 larvae from 14 species of Limacodidae were recorded on the two oak species in the 11 yr of sampling (Table 2). In the field, we were not able to reliably distinguish between two co-occurring species of *Tortricidia* (*T. pallida* and *T. flexuosa*, adults of which were reared in this study), so these two species were combined and treated as a single species group in all analyses. The larvae of a third species of *Tortricidia* (*T. testacea*) appear earlier in the season (late June; Wagner 2005) and therefore were unlikely to be included in our late season samples. *L. fasciola* was not reared from our sampling in the Missouri Ozarks, but does occur in the forests around St. Louis and was used in the laboratory feeding trials.

Averaged across years, total limacodid densities in the canopy of *Q. velutina* were twice as great as in the understory (Fig. 1; two-tailed $t_s = 2.57$, $N = 10$, $P = 0.030$). In contrast, average caterpillar densities on *Q. alba* were indistinguishable by stratum (two-tailed $t_s = 0.73$, $N = 10$, $P = 0.49$) and were intermediate between the two values for *Q. velutina.* Individual species patterns on *Q. velutina* either showed significantly higher densities on canopy foliage (*I. textula:* $T = 3$, $N = 9$, $P = 0.02$; *A. biguttata:* $T = 3$, $N = 10$, $P = 0.01$; *P. badia:* $T = 2$, $N = 7$, $P = 0.05$; Fig. 2) or showed

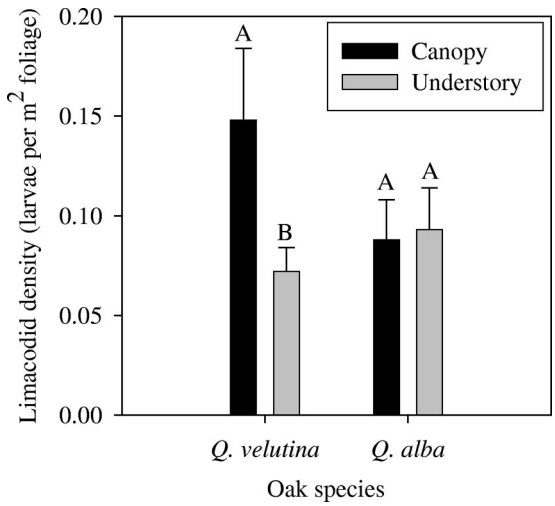

Fig. 1. Limacodid densities on oaks in two microhabitats (10-yr means ± SE) in southeast Missouri. For each oak species, means of strata with the same letter were not significantly different based on paired *t*-tests of log-transformed data.

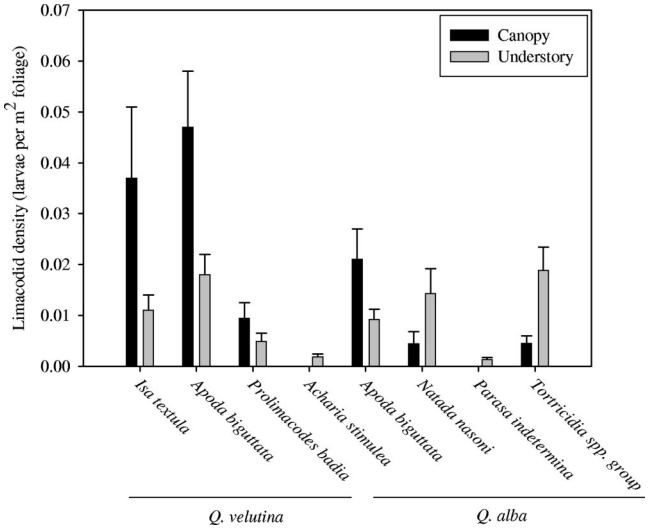

Fig. 2. Individual species densities on oaks in two microhabitats (10-yr means ± SE) in southeast Missouri. All comparisons between strata shown were significant using Wilcoxon's paired samples test on the rank-transformed data.

no difference (*A. spinuloides*, *E. delphinii*, *N. nasoni*, *Parasa chloris*, *Phobetron pithecium*, and *Tortricidia* spp.; all $P > 0.10$). The remaining species (*A. stimulea*, *Isochaetes beutenmuelleri*, *Monoleuca semifascia*, *Packardia geminata*, and *Parasa indetermina*) were in too low abundance to perform individual species analysis on *Q. velutina.* On *Q. alba*, five species showed significant differences between strata: *A. stimulea* ($T = 0$, $N = 7$, $P = 0.02$), *A. biguttata* ($T = 4$, $N = 9$, $P = 0.03$), *N. nasoni* ($T = 8$, $N = 10$, $P = 0.05$), *P. indetermina* ($T = 0$, $N = 6$, $P = 0.05$), and *Tortricidia* spp. ($T = 3$, $N = 9$, $P = 0.02$). With the exception of *A. biguttata*, all of these species were found in higher densities in the understory on *Q. alba* (Fig. 2), in direct contrast to the pattern on *Q. velutina.* The remaining species either showed no density differences between strata on *Q. alba* (*A. spinuloides*, *E. delphinii*, *I. textula*, *Isochaetes beutenmuelleri*, *P. pithecium*, and *P. badia*) or had insufficient densities for analysis (*M. semifascia*, *P. geminata*, and *Parasa chloris*). All species of slug caterpillars were found at least once on both oak species.

Further support for the glabrous host hypothesis came from the shorter-term study involving 20 host tree species in central Missouri. Density was significantly negatively correlated with density of trichomes on the bottom surface of leaves ($r_s = -0.50$; $N = 18$; $P = 0.0239$; Fig. 3A), and a similar trend was observed with density of trichomes on the top surface of leaves ($r_s = -0.423$; $N = 18$; $P = 0.065$; Fig. 3B).

There was considerable interannual variation in both total and individual species abundances (Table 2). The density of Limacodidae (all species combined) varied by more than an order of magnitude over just 3 yr, with a high in 1995 (≈0.2 larvae/m^2 or 306 total caterpillars) and a low in 1997 (0.01 larvae/m^2 or 11 total caterpillars). For an individual stratum, the highest recorded density was 0.4 larvae/m^2 in the canopy of *Q. velutina* in 1999.

Laboratory Feeding Trials. When given a choice of *Q. velutina* leaves, individual caterpillars were more likely to be found on canopy leaves, whereas those given a choice of *Q. alba* leaves were more frequently found on understory leaves ($\chi^2 = 8.99$; $P = 0.0027$). These choices were consistent for individual caterpillars across days ($P = 1.00$, Cochran-Mantel-Haenszel statistic for individual effects). After 3 d of exposure to leaves, caterpillars on *Q. velutina* tended to eat more from canopy leaves than from understory leaves (medians = 51 and 3 mm^2, respectively; $T = 109$; $P = 0.0916$), whereas those on *Q. alba* showed an apparent preference for understory leaves compared with canopy leaves (medians = 305 versus 0 mm^2, respectively; $T = 98$; $P = 0.065$); however, because neither test was significant at the $\alpha = 0.05$ level, these results should be viewed as trends.

When given a choice between intact and pubescence-removed bottom sides of *Q. velutina* understory leaves, 17 of 18 caterpillars were found on the experimental side of the leaf ($\chi^2 = 24.5$; $P < 0.0001$). As a result, caterpillars ate more from the pubescence-removed side (medians: 508 mm^2 versus 0 mm^2; $T = 41$; $P = 0.027$).

Discussion

Results from both the cross-stratum comparisons of limacodid densities for two host plants and comparisons across 20 species of woody plants were consistent with the glabrous host hypothesis suggested by Dyar (1899b) and elaborated on by Epstein (1988, 1995). As predicted, limacodid larvae were found in significantly lower densities on the highly pubescent understory leaves of *Q. velutina* compared with the smooth canopy leaves, whereas there was no overall effect of stratum on total densities on *Q. alba*, whose canopy and understory mature leaves are both glabrous. For

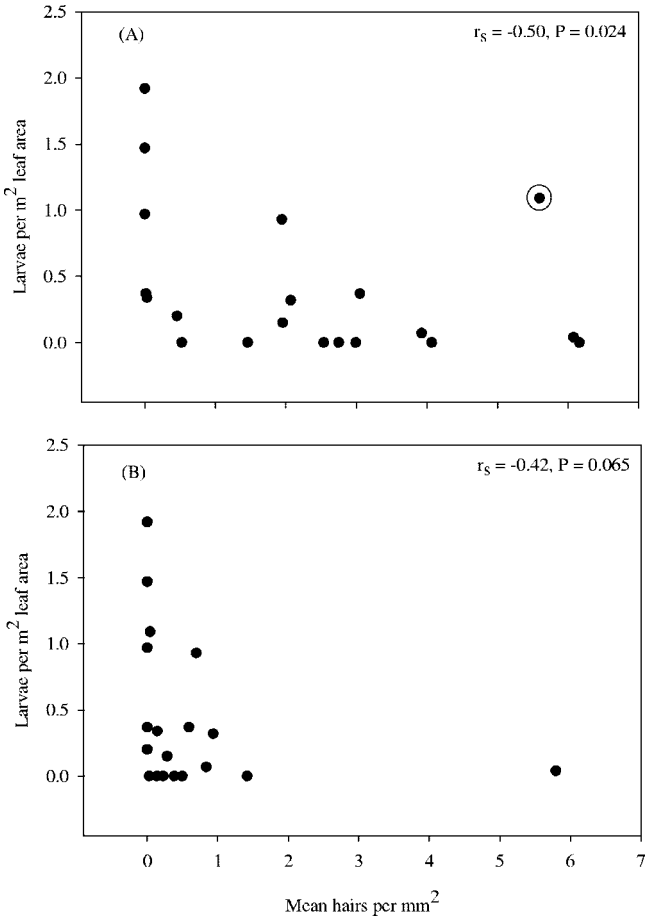

Fig. 3. Spearman rank correlations of limacodid caterpillar density and (A) lower surface pubescence density and (B) upper surface pubescence density for 20 species of woody plants. The circled point in A is *Q. imbricaria.*

the 20-tree species sample, density of slug caterpillars decreased with increasing pubescence, supporting the contention that slug caterpillars, while generalists with respect to plant taxonomy and plant chemistry, discriminate among plants based on leaf texture. Pubescence on the lower leaf surface was more strongly correlated with caterpillar density, where these slug caterpillars are more frequently found (Wagner 2005, R.J.M. and J.T.L., personal observation). *Q. imbricaria* is an obvious outlier in this pattern (Fig. 3A): it has many more caterpillars than one would expect by the degree of pubescence alone. Perhaps high leaf quality overrides the effect of pubescence for that host plant species.

We found larvae of all species in both the canopy and understory, contradicting the claims of Dyar (1896b, 1897c, 1898a) that slug caterpillars prefer understory foliage. Samples from the canopy-understory censuses were sufficiently large that we could test whether individual insect species varied between strata for each host plant. When significant, individual species densities on *Q. velutina* mirrored the combined-species pattern, with three species occurring in significantly higher densities in the canopy and no species having a higher density in the understory. Thus, interstratum differences in pubescence alone are sufficient to account for both the overall and individual density patterns. In contrast, four of the five species that showed significant differences among strata on *Q. alba* were in higher densities in the understory. This suggests that in the absence of differences in leaf pubescence, oviposition, and/or feeding site selection is determined by other leaf quality traits in the plant species. These leaf quality traits induce a feeding preference for understory leaves, as was shown in the interstratum feeding trials. Furthermore, we never recorded any limacodids on *Quercus* in the spring, when leaves are expanding and a deciduous fuzz is present on the leaves (particularly in *Q. alba*). Restriction of feeding to mature leaves may represent a phenological adaptation enabling these insect species to avoid pubescent leaves (Epstein 1988).

A variety of mechanisms might account for these host plant–specific differences in larval densities between strata and between pubescent and glabrous host plant species. Higher densities of larvae on glabrous leaves may simply reflect oviposition preferences. Epstein (1988) suggested that because limaco-

dids have characteristically flattened eggs as well as flattened ovipositor lobes, pubescent leaves could present a physical barrier to oviposition. Even if leaf pubescence does not prevent successful oviposition, consistently poor larval performance on pubescent leaves may constitute an important evolutionary force shaping oviposition site preferences through preference-performance linkages (Thompson 1988, Zalucki et al. 2002). The apparent feeding preferences of larval limacodids for nonpubescent leaves are coincident with their method of locomotion; both the excretion of semifluid silk (which aids in surface adhesion; Epstein 1995) and the loss of crochets on most of the abdominal prolegs would make movement (and feeding) potentially difficult on rough, pubescent surfaces. However, all but one of the limacodid species examined in the long-term study (*A. stimulea* being the exception) have been found on understory leaves of *Q. velutina*, indicating that leaf texture, while influencing relative abundance, does not entirely prohibit colonization and feeding of most species. Our finding that pubescence had a much stronger effect on abundance than on species richness is similar to what Andres and Connor (2003) reported in their study of manzanita herbivores.

Alternatively, survival of eggs and/or early instar larvae in different microhabitats that vary in abiotic conditions and/or natural enemy densities could produce the same patterns (Schowalter et al. 1986, Lowman 1992, Loeffler 1993) even if there were no interstratum differences in oviposition preference. Because larvae in the family are relatively sedentary and lack the ability to spin down on silk in response to enemy attack (Epstein 1995), movement of larvae between strata is unlikely. If natural enemy densities (Dahlsten et al. 1990) or attack (van Bael et al. 2003) vary between strata, variable caterpillar densities between strata (e.g., on *Q. velutina* in this study) could reflect differential survival from predators and/or parasitoids. Several lines of evidence suggest that natural enemies play an important role in limacodid biology: (1) many species possess urticating setae (e.g., *E. delphinii*, *P. indetermina*), particularly in early instars when larvae are thought to be most susceptible to predation and/or parasitism; (2) most stinging species also have bright, contrasting dorsal color patterns suggesting the evolution of aposematism in the group; and (3) nonstinging species are cryptic (e.g., resembling galls or leaf blotches; J.T.L., person observation), which, in combination with their slow movement and concealed feeding behavior (the mouthparts are completely concealed by the prothorax during feeding; Epstein 1995), suggests that visually oriented predators may have been or currently are an important source of mortality.

If differential predation between strata was responsible for the patterns in *Q. velutina*, however, we might expect the larvae found on *Q. alba* to show a similar reduced density in the understory compared with the canopy (assuming similar predator communities on the two host plants), which was not the case. In fact, four species were found in higher densities on understory *Q. alba*. Perhaps more importantly, the results of the two experimental feeding trials clearly indicate that larvae discriminate among leaves in selecting feeding sites. Caterpillars were more likely to avoid pubescent leaves or leaves from which pubescence had been experimentally removed. In turn, they fed more on nonpubescent leaves or leaves from which pubescence had been removed (see also Musetti and Neal 1997, Malakar and Tingey 2000, Fordyce and Agrawal 2001), suggesting that host plant traits (pubescence) play a primary role in determining patterns of host use in this assemblage. The degree to which the observed patterns are determined by oviposition preference for nonpubescent leaves versus differential survival on leaves that differ in pubescence is unknown at this time.

A final possible explanation for this pattern is that larvae (and/or ovipositing adults) are selecting microhabitats based on the nutritional quality of the foliage. A previous study examining the quality of canopy and understory leaves (Le Corff and Marquis 1999) found higher nitrogen in canopy than in understory *Q. velutina* leaves, whereas nitrogen content of *Q. alba* leaves did not differ among strata. However, the concentrations of condensed tannins, thought to be deterrent to oak herbivores (Feeny 1970), showed the opposite pattern, with highest concentrations (e.g., lowest quality) in *Q. velutina* canopy leaves and the lowest concentrations in *Q. velutina* understory leaves (*Q. alba* leaves from both strata were intermediate; Forkner et al. 2004). Because temperate limacodid larvae feed only in the late season (when leaf quality is typically at a seasonal low) and include in their diet a wide array of plants with entirely different classes of secondary compounds, it seems less likely that they would be sensitive to the relatively subtle interstratum differences in nutritional quality detected in these previous studies. It is notable that despite the great differences in secondary compound profiles represented by the 20 species sampled at Whiskey Creek Sheep Farm, leaf pubescence played a significant role in determining the number of attacking slug caterpillars found on these host plants. Experimental oviposition trials that examine female choice based on pubescence level and feeding trials that quantify feeding efficiency, development time, and pupal mass of larvae on foliage from different strata (Loeffler 1993) are needed to determine the importance of foliage quality relative to the other proposed factors.

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