

Structural and Taxonomic Components of Habitat Selection in the Neotropical Folivore *Lamponius portoricensis* (Phasmatodea: Phasmatidae)

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ABSTRACT *Lamponius portoricensis* Rhen is a folivorous neotropical walkingstick that is a common light-gap inhabitant of the tabonuco forest in Puerto Rico. Little is known concerning the spatial distribution of this phasmatid or the manner in which it selects habitats. Based on multiple regression analysis of a suite of taxonomic and structural characteristics of understory flora, we determined that the density of walkingsticks was associated with patches that exhibit high apparency values for *Piper treleaseanum* Britton & Wilson and *Symplocos martinicensis* Jacq., and low apparency values for *Dryopteris deltoidea* (Sw.) Kuntze. The total development of the understory regardless of taxonomic composition at 76 cm (2.5 ft) and 107 cm (3.5 ft) also contributes to high walkingstick density, based on correlative analyses. Moreover, nonparametric analysis suggests that *L. portoricensis* disproportionately occurs on *P. treleaseanum* (approximately twice as often as expected based on plant apparency). Despite these associations, only a third of the variation in walkingstick density is accounted for by this suite of floral characteristics. The low vagility of *L. portoricensis* may result in its having incomplete information about the abundance and distribution of forage plants, whereas patch-dynamic processes involving changes in quality of forage can confound the significance of apparency alone in predicting density. The production of aromatic attractants by *Piper* may act as the proximate cue affecting patch selection.

KEY WORDS understory, plant apparency, *Lamponius portoricensis*

ECOLOGY, AS THE STUDY of the abundance and distribution of organisms, has long focused on associations between organisms and their habitat. Although early definitions of the niche as the place where an organism exists (e.g., Grinnell 1917, 1928) have been supplanted by more abstract and intricate definitions (e.g., Hutchinson 1957, 1965; Whittaker & Levin 1975; Cohen 1978; Tilman 1982; Lomnicki 1988), even these concepts consider habitat as a critical axis of niche differentiation. Indeed, if dispersal limitation can be discounted, then habitat selection is the most parsimonious line of inquiry to pursue in understanding the distributional patterns of animal species, even before considerations of interspecific interactions (i.e., competition, predation, or parasitism) and the effect of physical or chemical parameters (Krebs 1985). The central position of habitat selection in population ecology is attested to by the recent collections of

papers exclusively dealing with the subject (see Rosenzweig [1987] and Orians [1991]).

Most animals do not occupy all their potential range even if they suffer no dispersal limitations. Moreover, not all areas of the range of a species support similar densities—at some scale, all taxa have aggregated spatial distributions. At the landscape level, the response of insects to disturbance dynamics is a product of colonizing ability and resource characteristics (Schowalter 1985). Colonizing ability includes both dispersal and host selection behavior, whereas the quality and quantity of resources affect subsequent population growth and persistence. As a result of these processes, different patches within an ecosystem support different densities of insects, and as patches undergo secondary succession the densities of insects change in accord with modification in the quality and quantity of resources. Changes in vegetation species composition and abundance, litter structure, and condition (attractiveness and suitability for reproduction) are the primary controls on the trajectories of changing insect abundance (see references in Schowalter [1985]).

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The structure and composition of the tabonuco forest within the Luquillo Experimental Forest of Puerto Rico is a product of the scale, intensity, and frequency of a variety of natural disturbance agents. In particular, tropical storms and hurricanes are thought to have a decisive impact in producing the melange of patches that characterize the landscape (Doyle 1981, 1982; Brokaw 1985; Weaver 1986). As a result of these patch-generating phenomena, light gaps are scattered throughout the forest and represent unique opportunities and challenges for exploitation by folivorous insects (Price 1975, Matthews & Matthews 1978, Wellington 1980, Schowalter et al. 1981). Although phasmatids are common herbivores in many tropical systems, little is known of their biology (Bedford 1978, Van Den Bussche et al. 1989).

The walkingstick *Lamponius portoricensis* Rehn is a large (up to 110 mm), common folivore and is potentially a keystone grazer in the tabonuco forest understory (Willig et al. 1986). In field circumstances, as well as in laboratory experiments (Sandlin Smith 1989, Sandlin & Willig 1993, M.R.W., unpublished data), *L. portoricensis* forages as a type D polyphagous herbivore (Cates 1980, Jermy 1984), consuming plant species that belong to a variety of families (e.g., Araliaceae, Leguminosae, Malvaceae, Piperaceae, Rubiaceae, Urticaceae). Forage plants used most frequently include *Piper treleaseanum* Britton & Wilson, *P. hispidum* Sw., *Urera baccifera* (L.) Gaud., and *Dendropanax arboreus* (L.) Decne & Planch., common understory constituents of light gaps. Food selection experiments (Sandlin Smith 1989; Sandlin & Willig 1993; M.R.W., unpublished data) consistently indicate that *U. baccifera* and *D. arboreus* are preferred forage, whereas *P. treleaseanum* is the least preferred. The demographic attributes of *L. portoricensis* are particularly adaptive to existence in small semi-isolated ephemeral habitats. In general, walkingsticks move <0.5 m per day and reach densities between 0.4 and 1.0 individuals per square meter; nymphs are philopatric, whereas adults (although wingless) constitute the dispersal stage. Even within a gap, *L. portoricensis* exhibits an aggregated spatial distribution that has been inferred to be affected by the nonrandom spatial distribution of forage species within the patch (Willig et al. 1986).

The purpose of this study was to determine if *L. portoricensis* exhibits a nonrandom spatial distribution at the mesoscale, evaluate the degree to which taxonomic or structural aspects of the habitat affect density, and identify those plant taxa that disproportionately serve as substrate or forage. Elsewhere, we document the dietary response of walkingsticks to changes in food abundance (M.R.W., unpublished data), age, sex, intraspecific variation in food quality, and preexposure to a particular food (Sandlin

Smith 1989, Sandlin & Willig 1993), as well as their demographic response to a large-scale disaster, Hurricane Hugo (Willig & Camilo 1991).

Materials and Methods

Study Area. The Luquillo Experimental Forest (LEF) of Puerto Rico occupies >1,150 ha, traverses elevations from 100 to 1,075 m, and includes four life zones: subtropical wet forest, subtropical rainforest, lower montane wet forest, and lower montane rainforest (Brown et al. 1983, Gines et al. 1984). Study sites were located within the subtropical wet forest (tabonuco forest) near El Verde Field Station (18° 10' N; 65° 30' W) at an elevation of 510 m; the dominant trees include *Dacryodes excelsa* Vahl. (tabonuco), *Sloanea berteriana* Choisy (motillo), and *Prestoea montana* (R. Grah.) Nichols (sierra palm). Mean monthly rainfall varies from 20 (March) to 40 (May) cm. Daily temperature varies little and averages 25.5°C. The terrain is steep, with cascading streams and luxuriant vegetation; before Hurricane Hugo in 1989, occasional light gaps punctuated an otherwise closed canopy.

Habitat Characteristics. Characterization of tropical rainforest understory by the density of plant species is problematic. Identification of individuals is not practicable because multiple stems frequently grow from a single root system, and some taxa (e.g., *Philodendron giganteum* Schott and *Marcgravia rectiflora* Tr.) are epiphytic, making ground stem counts inappropriate. Moreover, equal counts or densities of two different species do not necessarily indicate an equal contribution of substrate or food by those species. Therefore, a volumetric assessment of plant importance is a better representation of the structure and composition of the understory, especially as it relates to habitat selection by folivorous insects. We chose 60 rectangular quadrats (dimensions: 6.0 by 3.0 m; area: 18.0 m²) representing various microhabitats in the tabonuco forest for quantification of understory composition and structure. Surveys were conducted during the dry season between 15 and 20 March 1987. Each quadrat was surveyed along three parallel 5-m transects, with 1 m between adjacent transects. The three parallel transects were centered within the quadrat. At each transect, plant occurrence was surveyed at seven evenly spaced heights between 15 cm (0.5 ft) and 198 cm (6.5 ft). At each height, plants that occurred on the transect were tallied according to species and number of times they touched a string extending between endpoints of the transect (number of foliar hits, Cook & Stubbendieck 1986). The importance, or apparency (sensu Cates 1980), of a plant species in a particular site was estimated as the total number of foliar hits by that species at any height on all three transects

within the site. Only the 10 most common plants from all sites were used to characterize the general habitat of the tabonuco forest understory. Development of the understory (structure and composition) at each height was estimated as the sum of all foliar hits by all plant species at a particular height on all three transects. Total plant apparency was calculated as the total number of foliar hits in a given quadrat. Foliar height diversity (FHD) of each site was calculated using the formula for the Shannon function (Ludwig & Reynolds 1988):

$$\text{FHD} = - \sum_{i=1}^7 p_i \ln p_i,$$

where p_i is the ratio of apparency of all plant species at a height i to apparency of all plant species at all heights at the site. FHD is a measurement of the structural diversity of the understory. In summary, 19 habitat descriptors characterized each site: the apparency of each of 10 most common plant species, the development (total foliar hits regardless of plant species) of the understory at each of seven different heights, total plant apparency, and FHD.

Census Methodology. Walkingstick censuses were conducted within the same quadrats used to assess habitat characteristics. To minimize diel and monthly variation in sampling efficiency associated with walkingstick behavior, quadrats were censused only between 1900 and 0300 (times of maximum walkingstick activity) from 14 to 18 March (dry season). We thoroughly examined soil, litter, and all plant surfaces within the quadrat, up to a height of 1.98 m. Each quadrat was censused for a minimum of 30 min by the three of us. We tallied the number of walkingsticks per quadrat and recorded the substrate (including plant species) on which each was found. From these data, we estimated the local population density of walkingsticks within the quadrat as the minimum number known to be alive. Similarly, we tallied the number of times a walkingstick was captured on each plant species regardless of quadrat.

Statistical Analyses. Goodness of fit G statistics (Sokal & Rohlf 1981) were calculated via Biostat program GFIT (Pimentel & Smith 1986) to assess if walkingsticks exhibit a random spatial distribution (compared with a poisson distribution using average quadrat density of walkingsticks in our sample to estimate the parametric mean density). For this test, three classes of sites (those containing 9, 10, and 11 walkingsticks) were pooled so that $\leq 20\%$ of the classes contained fewer than five individuals (Sokal & Rohlf 1981). In addition, if walkingsticks have random distributions with respect to plant species, then the number of captures on each plant species should be proportional to the relative apparency of each

plant (ratio of the apparency of a species to the sum of the apparency of all species). This premise was evaluated by goodness of fit G statistics as well. For this test, the calculated expected frequencies of occurrence of walkingsticks, based upon plant apparencies, dictated that all but the 13 most commonly occurring plant species were pooled into seven classes to maximize degrees of freedom. This resulted in the formation of 20 classes, with only four having expected values < 5.00 .

The importance of the 19 habitat descriptors in accounting for variation in walkingstick density among quadrats was evaluated using forward entry (step-up) multiple regression analysis (SPSS-X Program REGRESSION) (SPSS 1988). With this method, the first variable (habitat descriptor) chosen in the regression equation has the largest positive or negative correlation with the dependent variable (number of walkingsticks per quadrat). Subsequent variables are added based on the absolute value of their partial correlation (discounting the effect of variables already selected for inclusion). In addition to the criterion of significance, we do not consider a variable to be important if it does not increase R^2 by at least 5% (Willig & Selcer 1989, Willig & Sandlin 1991). In this way, variables that account for significant and appreciable variation in walkingstick density are distinguished from variables that represent quantified characteristics of understory habitats that are not important in determining a reasonable amount of the variation in walkingstick density. We examined the correlation matrix between all pairs of variables because some variables exhibiting significant correlations with the density of walkingsticks may not be included in the final regression equation if they have high communality with previously entered descriptors.

Results

In total, 227 specimens of *L. portoricensis* were obtained from the 60 sites during nocturnal censuses. Forty-eight species of herbaceous and woody plants were censused and their apparencies were calculated. The 10 most common plant species and their relative apparencies are listed in Table 1. The other 38 species had a cumulative relative apparency of 0.21, with each species, on the average, having an apparency of < 0.01 . Thus, these species individually represent a minor portion of the taxonomic or structural components of the understory. Walkingsticks were obtained from 25 plant species recorded during daytime habitat characterization studies as well as from one additional plant species. Walkingstick density varied from 0 to 10 ($\bar{Y} = 3.8$; $S = \pm 2.96$) individuals per site. Individuals had a distinctly non random spatial distribution ($G = 61.44$; $df = 7$; $P < 0.001$; G test)

Table 1. Taxonomic classification and habits of the 10 most commonly found plant species in the tabonuco forest understory (those above the break), as well as dominant tree species and other plant species of interest (compiled from Valez [1957], Grisebach [1963], Little & Woodbury [1976], Little et al. [1977], Smith [1977], and Brown et al. [1983])

Species	Family	Habit	Relative apparency
<i>Piper treleaseanum</i> Britton & Wilson	Piperaceae	Shrub	0.31
<i>Prestoea montana</i> (R. Grah.) Nichols	Palmaceae	Palm	0.14
<i>Ichnanthus pallens</i> (Sw.) Kuntze	Gramineae	Herb	0.09
<i>Dacryodes excelsa</i> Vahl.	Burseraceae	Seedling, woody; tree	0.06
<i>Ruellia coccinea</i> (L.) Vahl.	Acanthaceae	Seedling, woody	0.05
<i>Danaea nodosa</i> Sm.	Equisetaceae	Herb	0.05
<i>Tetragastris balsamifera</i> (Sw.) Kuntze	Burseraceae	Seedling, woody	0.03
<i>Symplocos martinicensis</i> Jacq.	Symploaceae	Seedling, woody	0.02
<i>Guarea trichilioides</i> L.	Meliaceae	Seedling, woody	0.02
<i>Dryopteris deltoidea</i> (Sw.) Kuntze	Aspleniaceae	Fern	0.02
<i>Sloanea berteriana</i> Choisy	Eleocarpaceae	Seedling, woody; tree	0.02
<i>Dendropanax arboreus</i> (L.) Decne & Planch.	Araliaceae	Sapling; tree	0.03
<i>Urera baccifera</i> (L.) Gaud.	Urticaceae	Shrub	0.01
<i>Piper hispidum</i> Sw.	Piperaceae	Shrub	0.01
<i>Manilkara bidentata</i> (A. DC.) Chev.	Sapotaceae	Sapling	0.01
<i>Philodendron giganteum</i> Schott	Araceae	Vine	0.08
<i>Marcgravia rectiflora</i> Tr.	Marcgraviaceae	Vine	0.03

with a coefficient of dispersion ($CD = S^2/\bar{Y}$) equal to 2.30, indicating a contagious or clumped distribution.

The multiple regression analysis revealed that sites with high apparency values for *P. treleaseanum* and *Symplocos martinicensis* Jacq., as well as low apparency values for *Dryopteris deltoidea* (Sw.) Kuntze, attracted the highest densities of walkingsticks (Table 2). The simple correlation coefficient, r , measures the association between each habitat descriptor and the number of walkingsticks per site, whereas R^2 , the square of the multiple correlation coefficient, represents the amount of variation in number of walkingsticks that is explained by the combination of habitat descriptors included in the regression procedure to that step. Much of the variation in site density (67.5%) remained unaccounted for by the regression descriptors. Many of the 16 unselected habitat descriptors were not included in the final equation because they exhibited or approached significant correlations with the selected descriptors. Of these, four were significantly correlated with the density of *L. portoricensis* (apparencies of *Danaea nodosa* Sm., $r = -0.22$, $P = 0.049$, and *Ichnanthus pallens* [Sw.] Kuntze,

$r = 0.23$, $P = 0.041$; apparencies at 76 cm [2.5 ft], $r = 0.32$, $P = 0.007$, and at 107 cm [3.5 ft], $r = 0.28$, $P = 0.017$). Two of these were not included in the regression model because of high communality with selected variables: apparency at 76 cm (2.5 ft) is significantly correlated with *P. treleaseanum* apparency, and apparency at 107 cm (3.5 ft) is significantly correlated with apparencies of both *P. treleaseanum* and *D. deltoidea*. The absence of these four descriptors from the list of important variables occurs not because of intercorrelation with selected variables, but because they individually account for <5% of the variation in walkingstick density. Thus, they may be considered less important determinants of habitat selection by *L. portoricensis*.

Results from G tests corroborate those from the multiple regression. In general, *L. portoricensis* does not occur on plant taxa with the frequency predicted by their relative apparencies ($G = 218.7$; $df = 19$; $P < 0.001$, G test). In particular, walkingsticks occurred on *P. treleaseanum* more than twice as often as predicted by the relative apparency of *P. treleaseanum* (observed = 155, expected = 69.48; see Fig. 1), whereas both *I. pallens* (observed = 1, expected = 19.62) and

Table 2. Results of multiple regression analysis of *L. portoricensis* density as a function of 19 taxonomic and structural habitat descriptors

Descriptor	B	Significance	r	R^2	ΔR^2
<i>Piper treleaseanum</i>	0.137	0.002	0.354	0.125	0.125
<i>Symplocos martinicensis</i>	0.535	0.002	0.297	0.240	0.115
<i>Dryopteris deltoidea</i>	-0.589	0.010	-0.315	0.325	0.085
Constant	2.650	0.000			

The order of appearance of the three important variables (see text) corresponds with their entry into the final multiple regression equation. Significance refers to the hypothesis that a particular regression coefficient is zero (i.e., $H_0: \beta = 0$ versus $H_a: \beta \neq 0$). Codes are as follows: B , the regression coefficient in the final multiple regression equation; r , the simple correlation coefficient; R^2 , the multiple coefficient of variation (percentage variation in walkingstick density among sites that is explained by all variables in the equations at a particular step); ΔR^2 , the change in variation explained by the addition of a particular variable.

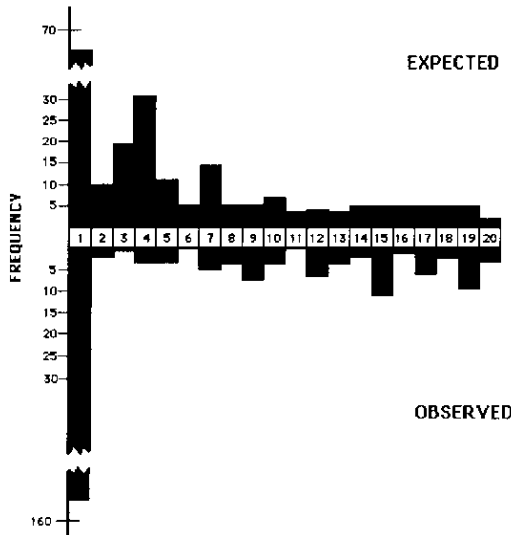


Fig. 1. Habitat selection by *Lamponius portoricensis* is indicated by the differences between observed and expected frequencies with which individuals were captured on particular plant species. The numbers on the ordinate represent particular plant species or groups of species. Plant species with low apparency (i.e., those on which walkingsticks were expected to be captured infrequently) required grouping to adhere to the assumptions of the G test. Numerical codes, which are species-specific, are as follows: 1, *Piper treleaseanum*; 2, *Danaea nodosa*; 3, *Ichnanthus pallens*; 4, *Prestoea montana*; 5, *Ruellia coccinea*; 6, *Dryopteris deltoidea*; 7, *Dacryodes excelsa*; 8, *Symplocos martinicensis*; 9, *Guarea trichiloides*; 10, *Tetragastris balsamifera*; 11, *Ingavera*; 12, *Philodendron giganteum*; and 13, *Hibiscusrosa-sinensis*. The other seven numerical codes (14–20) represent taxonomically artificial groupings of between 2 and 15 species.

P. montana (observed = 3, expected = 32.81) were less frequent sites of capture than predicted based upon apparency measures. Although the mechanisms whereby *L. portoricensis* selects habitats have not been elucidated, it is clear that walkingsticks have a hyperdispersed spatial distribution at the mesoscale, disproportionately occur on *P. treleaseanum*, disproportionately avoid *I. pallens* and *P. montana*, and reach highest density at sites characterized by high apparency for *P. treleaseanum* and *S. martinicensis* (seedlings) or low apparency for *D. deltoidea*.

Discussion

A recurrent theme in studies of habitat selection is that patch choice is affected by the array and density of preferred forage species (Stephens & Krebs 1986, Hanski 1989). This logically parallels evolutionary approaches to foraging theory—areas characterized by preferred

foods should support individuals with higher reproductive output. In ecological time, this should result in higher densities at sites dominated by preferred foods. In evolutionary time, this should result in the development of behavioral or ecological characteristics that facilitate the identification of and dispersal to such resource-rich patches. Given such a scenario, one would expect *L. portoricensis* to occur disproportionately on forage species that are preferred foods, such as *U. baccifera* and *D. arboreus* (Sandlin Smith 1989; Sandlin & Willig 1993; M.R.W., unpublished data), and avoid those that are not. In this context, the disproportionate occurrence of walkingsticks on *P. treleaseanum* and the importance of *P. treleaseanum* as a predictor of walkingstick density constitute a dilemma because this plant species is consistently a least-preferred food in selection experiments. Moreover, neither *U. baccifera* nor *D. arboreus* appears as an important contributor to habitat selection as evaluated by G tests or multiple regression analyses.

At least in part, this dilemma is resolved based upon considerations of the rarity of the most-preferred foods throughout the landscape and the patch-dynamic processes that occur during recovery from disturbance. Preferred foods were quite rare in our study sites (*U. baccifera* [relative apparency = 0.002] and *D. arboreus* [relative apparency = 0.007]), whereas *P. treleaseanum* was the most abundant understory taxon (relative apparency = 0.306). The consequences of specialization on rare preferred foods would undoubtedly result in a lower-carrying capacity for *L. portoricensis*. Perhaps individuals that selectively exploit preferred foods upon encounter but are willing to consume other foods as well would contribute on average more offspring to future generations than would individuals with a more stenophagic diet. Indeed, patch-use models predict that lower-quality foods should be selected if travel time between patches of high-forage quality is long (Stephens & Krebs 1986) as would occur if the diet were restricted only to *U. baccifera* and *D. arboreus*. However, models do not predict disproportionate use of such abundant but lower-quality foods.

Extrapolation of laboratory experiments to field situations must be done within the limitations of the experimental design used in the laboratory. More specifically, *P. treleaseanum* was a least-preferred food only in comparison with the other foods used in feeding trials, not in comparison with all other potential foods that are available in the understory. Thus, *P. treleaseanum* may be a "preferred food" compared with the array of potential forage species in the forest, but less beneficial than either *U. baccifera* or *D. arboreus*. If this is so, then *P. treleaseanum* should (and does) dominate the multiple regression analysis and goodness of fit G test because of its

greater relative apparency throughout the landscape. Comparison of the observed and expected values from the goodness of fit G test also corroborates that foods more preferred than *P. treleaseanum* in food selection experiments disproportionately serve as substrate or forage compared with their relative apparency (observed and expected, respectively, for *D. arboreus* [8.0, 1.5] and *P. hispidum* [6.0, 3.2]) or are so rare that stochastic processes would likely produce the observed relationship (*U. baccifera* [0, 0.4]).

Distinction of the proximate cues that indicate habitat suitability and ultimate factors responsible for high fitness is problematic in many field studies of habitat selection. Moreover, studies such as ours cannot independently uncouple correlated habitat characteristics. All three of the important habitat attributes in the multiple regression analyses were taxon-specific (apparencies of *P. treleaseanum*, *S. martinicensis*, and *D. deltoidea*); nonetheless, the apparencies of some of these plants were significantly correlated with structural attributes of the understory (apparencies at 0.76 and 1.07 m). As a result, we cannot unequivocally demonstrate the hegemony of taxonomic or structural attributes in influencing habitat selection in *L. portoricensis*.

In addition to the methodological constraints of nonmanipulative studies, the complexity of patch-dynamic processes could lead to similar phenomena. For example, stands of herbaceous shrubs that dominate light-gap situations can persist for a number of years after canopy closure. During such secondary succession, plants tolerate a range of soil nutrient regimes. However, the consequent change in nutritional quality of foliage and its translocation throughout the plant may represent an important complication in understory plant-insect interactions (Vitousek 1985). In effect, plant densities per se may be less important than spatial and temporal variation of nutritional quality in understanding the habitat associations of some herbaceous insects, especially those that are gap specialists.

When organisms are small or tardigrade, they tend to perceive the environment in a coarse-grained fashion (Levins 1968), often unable to exploit high-value patches because they are unaware of the existence of such patches. This represents a critical challenge for insects, especially nonvolant walkingsticks, which specialize on early successional species or gap specialists, yet have low velocities (Willig et al. 1986). Detection of new light gaps becomes critical because gap closure heralds a decrease in the abundance and possibly quality of forage species. Members of the Piperaceae frequently are gap specialists (Fleming 1985) and are characterized by the production of aromatic compounds (Baldwin & Schultz 1988) that may act as directional cues that facilitate the detection of recently created light gaps. This, too, may contribute to the im-

portance of *P. treleaseanum* in correlative analyses and explain the disproportionate occurrence of walkingsticks on *P. treleaseanum*.

The significantly clumped spatial distribution of *L. portoricensis* is clearly linked to habitat selection involving various taxonomic and structural attributes of the landscape. However, only a third of the variation in insect numbers is accounted for by the multiple regression. Differences in plant quality associated with patch regeneration could reduce the association between these habitat characteristics and walkingstick density. Perhaps equally important, habitat selection itself may be density-dependent (see Pulliam & Danielson [1991] and references contained therein): at high overall densities, walkingstick numbers may not vary as greatly between patches of markedly different quality. In both ideal free (Fretwell & Lucas 1970) and ideal preemptive distributions (Pulliam & Danielson 1991), the detection of habitat selection via correlative methods could become compromised during population peaks associated with density cycles or productive years. Indeed, if the assumption of identical fitness-site quality relationships is relaxed in these models, the previously high-quality habitats may actually support lower densities of insects than the previously considered poor-quality habitats (M.R.W. & M. McGinley, unpublished data). In such circumstances, relative habitat quality itself is density-dependent.

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