STRUCTURAL AND TAXONOMIC CORRELATES OF HABITAT SELECTION BY A PUERTO RICAN LAND SNAIL

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ABSTRACT—Although terrestrial molluscs make important contributions to the taxonomic and functional diversity of tropical systems, little is known about their ecology. *Caracolus caracolla* is a large terrestrial snail, common in a wide variety of habitats on Puerto Rico, including the tabonuco rain forest. To determine if this snail exhibits habitat selection, we surveyed 19 taxonomic and structural attributes of the understory, as well as snail abundance, in 60 sites within the tabonuco rain forest during the dry season. *Caracolus caracolla* had a clumped spatial distribution, and was associated more often than expected by chance with the shrub, *Piper glabrescens*, and less often than expected on three other common understory plants. Although much of the variation in snail density (73.4%) appeared unrelated to habitat descriptors, patches of forest with abundant ground cover at 0.15 m or high plant apparency (foliar development) at 1.98 m harbored high snail densities. The spatial distribution of *C. caracolla* was linked to microhabitat conditions that reduce the likelihood of desiccation. We hypothesize that smaller snails occupy areas of the understory where the likelihood of desiccation is reduced, whereas larger individuals, less encumbered by physiological constraints related to desiccation, expand their niche to include upper reaches of the understory where they take advantage of additional resources and enhance the likelihood of mate encounter.

RESUMEN—Si bien es sabido que los moluscos terrestres contribuyen de manera importante a la diversidad funcional y taxonómica en ecosistemas tropicales, es poco lo que se conoce de su ecología. *Caracolus caracolla* es un caracol terrestre de gran tamaño, común en una amplia variedad de hábitats en Puerto Rico, entre ellos el bosque tropical de tabonuco. Con el objetivo de determinar si esta especie muestra selección de hábitat, se muestrearon 19 características taxonómicas y estructurales del sotobosque y se estimó la abundancia del caracol en 60 sitios dentro del bosque tropical de tabonuco. El muestreo se llevó a cabo durante la estación seca. *Caracolus caracolla* mostró una distribución espacial agrupada, se encontró asociado con mayor frecuencia de la esperada por azar con el arbusto *Piper glabrescens* y menos de lo esperado con otras tres especies vegetales del sotobosque. Aunque mucha de la variación en densidad (73.4%) de caracoles parece no tener relación con los descriptores de hábitat seleccionados, en parches de bosque con cobertura abundante al nivel de 0.15 m, o de alto desarrollo foliar al nivel de 1.98 m, se encontró una mayor densidad de caracoles. La distribución espacial de *C. caracolla* está aparentemente ligada a condiciones del microhábitat que tienden a reducir la probabilidad de desecación. Nuestra hipótesis es que los caracoles más pequeños ocupan aquellas áreas del sotobosque donde la probabilidad de desecación es reducida, en tanto que individuos mayores, menos sujetos a restricciones fisiológicas relacionadas con la desecación, expanden su nicho para incluír zonas más altas del sotobosque donde pueden aprovechar recursos adicionales disponibles en esta área así como aumentar su probabilidad de reproducirse.

Ecological research has long focused on relationships between organisms and their habitat. Early definitions of the ecological 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 and Levin, 1975; Cohen, 1978; Tilman, 1982; Lomnicki, 1988). Nonetheless, these contemporary concepts also consider habitat as a critical axis of niche differentiation that can facilitate coexistence of species. In fact, if dispersal limitation can be discounted, habitat selection is the most parsimonious line of inquiry to pursue in understanding distributional patterns. This is true, even before considerations of interspecific interactions (i.e., competition, predation, or parasitism) and the effect of physical or chemical parameters (Krebs, 1985) become necessary. Moreover, the importance of habitat selection to the conceptual development of contemporary ecology is evidenced by recent compendia that focus exclusively on the subject (see Rosenzweig [1987] and Orians [1991]).

Several factors (e.g., competition, predation, parasitism) prevent a species from occupying all of its potential range, even if dispersal is unlimited. In addition, individuals are not distributed evenly throughout a species' range; they are clumped at some geographic scale. At the landscape level, the response of invertebrates to disturbance dynamics is a product of colonizing ability and resource characteristics (Schowalter, 1985) as well as the nature of the disturbance itself (Willig and McGinley, 1998). 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 a species. As patches undergo succession, densities change to parallel modifications in the quantity and quality of resources. Changes in vegetation and litter structure (species composition and abundance), as well as changes in the condition of litter and vegetation are the primary controls on the trajectories of changing invertebrate abundance (see references in Schowalter [1985]).

The small homeranges and low mobility of terrestrial snails suggest that they should be likely candidates to respond to environmental heterogeneity (Alvarez and Willig, 1993; Secrest et al., 1996; Willig et al., 1997). This is particularly true for regions, such as the Caribbean, that are structured by frequent or large-scale disturbances (Waide and Lugo, 1992). For example, it is well-documented that the

structure and composition of the tabonuco rain forest of Puerto Rico is a product of the scale, intensity, and frequency of a variety of natural disturbance agents (see Walker et al., 1991, 1996). In particular, tropical storms and hurricanes have a decisive impact in producing the melange of patches that characterize the landscape (Doyle, 1981, 1982; Lugo and Waide, 1993; 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 herbivorous and saprophytic invertebrates (Price, 1975; Matthews and Matthews, 1978; Wellington, 1980; Schowalter et al., 1981; Brokaw, 1985).

After arthropods, land molluscs are the most diverse animal taxon in terrestrial ecosystems (Russell-Hunter, 1983). In addition to their numerical importance, their contribution to ecosystem processes is reflected in their functional diversity as detritivores, herbivores, and carnivores (Purchon, 1977). Nonetheless, little is known about terrestrial mollusc ecology and most work focuses on a few temperate zone species. The land snail, *Caracolus caracolla*, is a large (maximum diameter, 60.0 mm), common (Willig and Camilo, 1991; Alvarez and Willig, 1993; Cary, 1992; Willig et al., 1997) invertebrate that is distributed in many habitats throughout Puerto Rico (Hernandes de Arroyo, 1974; Heatwole and Heatwole, 1978). Most ecological research on the species is limited to the tabonuco (*Dacryodes excelsa*) rain forest, where it coexists with 34 other snail species at a density of approximately 400 individuals per ha (Willig and Camilo, 1991). Individuals may live up to 15 years and consume mostly diatoms, wood cells, plant hairs, leaf cells, and mycelia (Heatwole and Heatwole, 1978; Lodge, 1996). Juvenile and adult snails spend diurnal hours in different microhabitats. More specifically, juveniles occur under leaf litter, stones, or logs, whereas adults frequently occur on tree trunks. During the dry season, even adults seek refuge in tree holes or root knots and under litter (Heatwole and Heatwole, 1978). Data on the contribution of invertebrates to the food web in the tabonuco forest (Garrison and Willig, 1996) suggest that snails, like many animals inhabiting islands, enjoy reduced predation pressure. Small snails with relatively soft shells may occasionally be eaten by omnivorous

birds such as the pearly-eyed thrasher (*Margarops fuscatus*) or the red-legged thrush (*Mimocichla plumbea*), whereas the most likely predator of larger snails with hard shells is the land crab, *Epilobocera situatifrons*.

In a comparative study of the distribution and abundance of common terrestrial snails in the tabonuco rain forest of Puerto Rico, Alvarez and Willig (1993) documented that *C. caracolla* responded to patches caused by treefall gaps. In particular, *C. caracolla* was twice as abundant, on average, in surrounding forest than in treefall gaps (4.4 individuals versus 2.1 individuals per 32 m^2). Similarly, Willig and Camilo (1991) documented that *C. caracolla* responded to the changes in the structure and composition of the tabonuco rain forest in the aftermath of Hurricane Hugo (18 September 1989). In the tabonuco forest in general, average snail densities significantly decreased to less than 25% of their pre-hurricane levels (3.1 to 0.7 individuals per 78.54 m^2), although no significant difference in size class distribution occurred between pre- and post-hurricane surveys. In 1994, density of *C. caracolla* (8.9 individuals per 78.54 m^2) exceeded that prior to the hurricane (Secrest et al., 1996; Willig et al., 1997). Detailed information concerning the autecology (e.g., demography, homerange, habitat selection) of *C. caracolla* two years after the impact of Hurricane Hugo is presented by Cary (1992) and Cary and Willig (unpubl. ms.).

The purposes of our research were to 1) determine if *C. caracolla* exhibits a nonrandom spatial distribution, 2) identify those plant taxa that disproportionately serve as substrate or forage, and 3) evaluate the degree to which taxonomic or structural aspects of habitat affect variation in density. In addition, this research provides important comparative data for studies that evaluate the effect of disturbance on snail populations because it was conducted 1.5 years prior to the impact of Hurricane Hugo.

METHODS—*Study Area*—The Luquillo Experimental Forest of Puerto Rico occupies over 1,150 ha, traverses elevations from 100 to 1,075 m, and includes four life zones: subtropical wet forest, subtropical rain forest, lower montane wet forest, and lower montane rain forest (Brown et al., 1983; Gines et al., 1984). Study sites were located within the subtropi-

cal wet forest (tabonuco rain forest) near El Verde Field Station (18°10'N; 65°30'W) at 350 m; the dominant trees include *Dacryodes excelsa* (tabonuco), *Sloanea berteriana* (motillo), and *Prestoea montana* (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. Prior to Hurricane Hugo, occasional light gaps interrupted an otherwise closed canopy. Reagan and Waide (1996) provide extensive information on the flora, fauna, and environmental characteristics of the tabonuco rain forest at El Verde.

Habitat Characteristics—As discussed in detail by Willig et al. (1993), characterization of tropical rain forest understory by the density of plant species is problematic. Identification of individuals is difficult because multiple stems may grow from a single root system and some species (e.g., *Philodendron giganteum* and *Marcgravia rectiflora*) are epiphytes, making counts of ground stems inappropriate. Moreover, equal counts or densities of different species do not necessarily indicate that they make an equal contribution of substrate or food. As a consequence, a volumetric assessment of plant apparency (Cates, 1980) is a better representation of the composition and structure of the understory, especially as it relates to habitat selection by snails.

Between 15 and 20 March 1987, we quantified understory composition and structure in 60 rectangular quadrats (dimensions, 6.0 m by 3.0 m; observation grain 18 m^2 sensu Weins, 1990) representing various microhabitats in the tabonuco rain forest at El Verde Field Station (South of the Quebrada Sonadora). Each quadrat was surveyed along three parallel 5 m transects, with 1 m spacing between adjacent transects. The three parallel transects were centered within the quadrat. At each transects, plant apparency was surveyed at seven evenly-spaced heights between 0.15 m (0.5 ft.) and 1.98 m (6.5 ft.) in order to volumetrically assess habitat characteristics. 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 and Stubbendieck, 1986). The importance (apparency) 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 ten most common plants from all sites were used to characterize the general habitat of the tabonuco rain forest. The development of the understory 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 at a given site. Foliar height diversity (FHD) of each site

was calculated using the Shannon diversity index (Ludwig and Reynolds, 1988),

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

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. Because each site is characterized by foliar development at seven heights in the understory, FHD is a measurement of the structural evenness of the understory rather than an estimate of diversity per se. In summary, 19 habitat descriptors characterized each site: the importance of the ten most commonly occurring plant species, the development of the understory at seven different heights, total plant apparency, and FHD.

Census Methodology—Snail censuses were conducted within the same quadrats that were used to assess habitat characteristics. To minimize diel and monthly variation in sampling efficiency associated with snail behavior, quadrats were censused only between 1900 and 0300 hours (times of maximum snail activity) during the dry season. Three field investigators 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 minutes. We tallied the number of snails per quadrat and recorded the substrate (including plant species) from which each was obtained. From these data, we estimated the local population density of snails within the quadrat as the minimum number known to be alive. Similarly, we tallied the number of times a snail was captured on each plant species regardless of quadrat.

Statistical Analyses—Goodness of fit G-statistics (Sokal and Rohlf, 1981) were calculated via Biostat program GFIT (Pimentel and Smith, 1986) to assess whether snails exhibit a random spatial distribution (based on a Poisson distribution using average density of snails per quadrat to estimate the parametric mean density). For this test, six classes of sites (those containing 9 to 14 snails) were pooled so that ≤20% of the classes had expected frequencies less than 5.00 (Sokal and Rohlf, 1981). Additionally, if snails 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 snails, based upon plant apparencies, dictated that all but the ten most commonly-occurring plant species should be pooled into eight classes to maximize degrees of freedom. This resulted in the formation of 18 classes with only three having expected values less than 5.00.

The importance of the 19 habitat descriptors in

accounting for variation in snail density among quadrats was evaluated using forward entry (step-up) multiple regression analysis (Program REGRESSION, SPSS Inc., 1988). With this method, the first variable (habitat descriptor) chosen in the regression equation had the largest positive or negative correlation with the dependent variable (number of snails per quadrat). Subsequent variables were added based upon the absolute value of their partial correlation (i.e., discounting the effect of variables already selected for inclusion). This procedure terminated when no additional variables satisfied the criterion probability of 0.05. In addition to the criterion of significance, we did not consider a variable to be important if it did not increase R^2 by at least 5% (Willig and Selcer, 1989; Willig and Sandlin, 1991; Willig et al., 1993). In this way, variables that accounted for significant and appreciable variation in snail density were distinguished from those that represented characteristics of understory habitats which were not important in determining snail density. However, some variables that exhibited significant correlations with the density of snails may not have been included in the final regression equation if they had high communality with descriptors that were already in the equation. We examined the correlation matrix between all pairs of variables to evaluate the degree to which this phenomenon may have influenced the results of the multiple regression analysis.

RESULTS—A total of 187 specimens of *C. caracolla* was obtained from the 60 sites during nocturnal censuses. In addition, the apparencies of 48 species of herbaceous and woody plants were calculated based on survey data. The ten most common plant species differed in relative apparency from 0.024 to 0.311 (Table 1). The other 38 species had a cumulative relative apparency of 0.21, with each species, on average, having an apparency of less tan 0.01. Thus, these species individually represented a minor portion of the taxonomic or structural components of the understory. Snails were obtained from 23 plant species recorded during habitat characterization studies. Snail density differed from 0 to 13 (Y = 3.25; S = ±2.97) individuals per quadrat. Individuals had a distinctly non-random spatial distribution (G-test: G = 34.36; df = 7; P < 0.001) with a coefficient of dispersion (CD = S^2/Y) equal to 2.72, indicating a contagious or clumped distribution.

Multiple regression analysis revealed that sites with high apparencies at 1.98 m and 0.15

TABLE 1—Taxonomic classification, habits and relative apparency of the ten most common plant species surveyed in the understory of the tabonuco rain forest (those above the break), as well as dominant tree species and other plant species of interest (compiled from Brown et al. [1983], Lawrence [1996], Little and Woodbury [1976], Little et al. [1977], Smith [1977]).

Species	Family	Habit	Relative apparency
Piper glabrescens	Piperaceae	shrub	0.311
Prestoea montana	Palmaceae	palm	0.147
Ichnanthus pallens	Poaceae	grass	0.088
Dacryodes excelsa	Burseraceae	seedling, woody; tree	0.065
Ruellia coccinea	Acanthaceae	seedling, woody	0.052
Danaea nodosa	Marattiaceae	fern	0.046
Tetragastris balsamifera	Burseraceae	seedling, woody	0.032
Symplocos martinicensis	Symploaceae	seedling, woody	0.024
Guarea guidonia	Meliaceae	seedling, woody	0.024
Thelypteris deltoidea	Thelypteridaceae	fern	0.024
Philodendron giganteum	Araceae	vine	0.021
Piper hispidum	Piperaceae	shrub	0.014
Dendropanax arboreus	Araliaceae	sapling; tree	0.007
Marcgravia rectiflora	Marcgraviaceae	vine	0.007
Sloanea berteriana	Eleocarpaceae	seedling, woody; tree	0.005
Urera baccifera	Urticaceae	shrub	0.002
Manilkara bidentata	Sapotaceae	sapling	0.001

m attracted high densities of snails (Table 2). The simple correlation coefficient, r, measures the association between each habitat descriptor and the number of snails per site. R^2, the

TABLE 2—Results of multiple regression analysis of *C. caracolla* density as a function of 19 taxonomic and structural habitat descriptors. The order of appearance of the two important variables 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$_0$: β = 0 versus H$_a$: $\beta \neq 0$). Codes are: β, the regression coefficient in the final multiple regression equation; r, the simple correlation coefficient; R^2, the multiple coefficient of variation (% variation in snail density among sites that is explained by all variables in the equation at a particular step); ΔR^2, the change in variation explained by the addition of a particular variable.

Descriptor	B	Significance	r	R^2	ΔR^2
Height at 1.98 m	0.561	<0.001	0.384	0.147	0.147
Height at 0.15 m	0.179	0.004	0.240	0.266	0.119
Constant	0.442	0.582			

multiple correlation coefficient, represents the amount of variation in number of snails that is explained by the combination of habitat descriptors included in the regression procedure to that step. Most of the variation in site density (73.4%) remained unexplained by regression descriptors. Some of the 17 unselected habitat descriptors were not included in the final equation because they exhibited or approached significant correlations with the selected descriptors. Of these, five were significantly correlated with the density of *C. caracolla*, (apparencies of *Prestoea montana*, r = 0.303, P = 0.009, and *Guarea guidonia*, r = 0.254, P = 0.025; apparencies at 1.37 m (4.5 ft.), r = 0.258, P = 0.023, and 1.68 m (5.5 ft.), r = 0.360, P = 0.002; and total apparency, r = 0.365, P = 0.002). Apparency of *Prestoea montana* and total apparency were correlated with both selected descriptors; apparencies at 1.37 m and 1.68 m were correlated with apparency at 1.98 m; and apparency of *Guarea guidonia* was correlated with apparency at 0.15 m.

Results from G-tests corroborate those from multiple regression (Fig. 1). In general, snails did not occur on plant taxa with the frequency predicted by their relative apparencies (G-test:
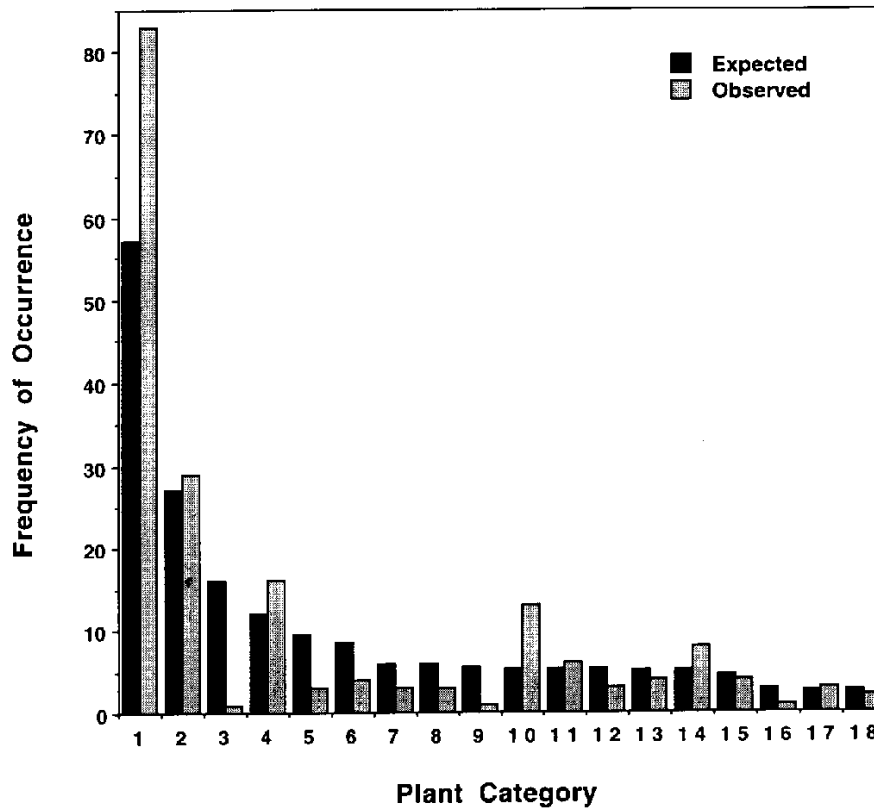
Fig. 1—Habitat selection by *C. caracolla* is indicated by the difference between observed and expected frequencies with which individuals were captured on particular plant taxa. The numbers on the ordinate represent particular plant species or groups of species. Plant species with low apparency (i.e., those on which snails were expected to be captured infequently) required grouping to adhere to the assumptions of the G-test. Numerical codes, which are species specific, are as follows: 1, *P. glabrescens*; 2, *P. montana*; 3, *I. pallens*; 4, *D. excelsa*; 5, *R. coccinea*; 6, *D. nodosa*; 8, *Tetragastris balsamifera*; 15, *Symplocos matinicensis*, 16, *Hibiscus rosa-sinensis*; and 18, *Piper hispidum*. The other 8 numerical codes represent taxonomically eclectic groupings of between 2 and 12 species.

$G = 66.91$; $df = 17$; $P < 0.001$). In particular, *C. caracolla* occurred on *P. glabrescens* more often than predicted by the relative apparency of *P. glabrescens* (observed = 83, expected = 57.24), whereas *Ichnanthus pallens* (observed = 1, expected = 16.20), *Ruellia coccinea* (observed = 3, expected = 9.52), and *Danaea nodosa* (observed = 4, expected = 8.46) were less frequent sites of capture than predicted based on apparency measures.

Discussion—A recurrent theme in studies of habitat selection is that the choice of a particular patch is affected by the array and density of preferred forage species as well as by the

costs associated with foraging in the patch (Stephens and Krebs, 1986; Hanski, 1989). This logically parallels evolutionary approaches to foraging theory because 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 behavioral or ecological characteristics that facilitate the identification of and dispersal to resource-rich patches. Consequently, *C. caracolla* should occur disproportionately on forage species that are themselves preferred foods or that harbor preferred food such as diatoms or fungi, es-

pecially if predation risk, the likelihood of desiccation, or other costs are equivalent in all patches.

In contrast to expectation, most (73.4%) of the spatial variation in snail density was not related to variation in structural or taxonomic attributes of the understory that we measured or that were associated with characteristics that we measured. At a cursory level, this may suggest that *C. caracolla* does not exhibit strong habitat selection. Alternatively, patch selection may be related primarily to vertical components of habitat, with strata below 2 m representing more preferred sites than do strata above 2 m. This corresponds to the results of earlier work that showed *C. caracolla* most frequently occupied the understory from ground level up to 2 or 3 meters (Heatwole and Heatwole, 1978; Willig and Camilo, 1991; Alvarez and Willig, 1993).

In a parallel study focusing on a folivorous stick insect, *Lamponius portoricensis*, less than a third of the spatial variation in density was explained by the identical suite of habitat characteristics (Willig et al., 1993). Like the scenario for *L. portoricensis*, the low vagility of *C. caracolla* may result in individuals having only incomplete information about the abundance and distribution of forage plants. Moreover, patch-dynamic processes during secondary succession alter the microclimatic and nutrient environment of plants. The physiological response of plants to the changing abiotic environment involves translocation of nutrients and defense compounds. Consequently, the quality of forage plants may be site-specific (Sandlin and Willig, 1993), decreasing the strength of association between snail density and apparency of particular plant species.

Avoidance of *I. pallens* may reflect a structural limitation. This grass lacks well-developed supportive tissue and may be incapable of supporting the weight of most snails, with the exception of the smallest individuals. Preferential occurrence on *P. glabrescens* may be a consequence of the foliar development of this shrub at 0.15 m, where microclimatic conditions are more favorable, especially for smaller snails. Moreover, *P. glabrescens* may provide the most direct access to upper levels of the understory by larger snails occupying diurnal retreats at ground level. Of course, the quality of this plant as a forage, or the quality of the micro-

flora that colonize its surfaces, may influence its selection by *C. caracolla* as well.

Although habitat selection at the scale of our study is not strong, snails do significantly differentiate among sites in two-dimensional space as evidenced by the results from both multiple regression and G-tests. Selection of sites is related to development of understory in a vertical dimension, with snails occupying habitats with high apparency near ground (0.5 m) or at the upper reaches of the understory (1.37 to 2 m). The lack of significance between FHD (a measure of evenness because 7 heights can only be sampled in the understory) and the density of snails, along with the significance of apparency at particular heights (e.g., 0.15 m and 1.98 m), emphasizes the importance of specific understory physiognomies to invertebrate abundance. The location of foliar development is more important than vertical variation in foliar development. Elevated densities of snails at sites with high apparency near ground level may primarily be attributable to the behavior of nonreproductive individuals in the population. Nonreproductive and therefore smaller snails may prefer areas with dense ground cover because they support a moist microclimate, especially during the dry season. Additionally, the potential role of microsite moisture is suggested by the significant correlation between densities of *C. caracolla* and the apparency of the sierra palm, *P. montana*. Sierra palms are well-documented to occur in moist microsites, especially areas with poorly drained soils (Bannister, 1970). In addition, water loss by snails may be directly correlated to the extent and duration of their movement because respiration rates in *C. caracolla* are twice as great when soft tissues are extended while moving than when soft tissues are retracted within the shell (Stiven, 1970). The emerging view is that a minimization of travel time while foraging closer to ground cover may effectively reduce water loss via respiration or mucus secretion.

Reproductive snails, and hence larger individuals, may be better able to retain moisture than can their smaller counterparts, if only because of their lower surface area-to-volume ratios. In addition, adults may derive a selective advantage in locating mates by foraging higher in the understory. Indeed, most copulating pairs of snails at El Verde are found between

1.5 and 2.0 m above the forest floor (Cary, 1992; Willig, pers. obser.). Because epiphytic algae that occur on *P. montana* attain highest densities on 2.5 year old fronds (Watson, 1970), it is likely that the upper reaches of the understory offer enhanced foraging opportunities for larger snails that can absorb the travel costs.

Both macro- and micro-spatial studies of *C. caracolla* have suggested that moisture plays a dominant role in determining distributional patterns (Hernadez de Arroyo, 1974; Heatwole and Heatwole, 1978; Cary, 1992; Alvarez and Willig, 1993), even though the species occurs in moist tropical environments. Our work identified and characterized the distinctly nonrandom spatial distribution of *C. caracolla* within the understory of the tabonuco rain forest. In addition, we showed that densities of *C. caracolla* are associated with structural and taxonomic attributes of the understory that primarily reflect considerations of moisture. Finally, we hypothesize that smaller individuals are constrained to forage low in the understory as a consequence of physiological limitations, directly in terms of water balance, or indirectly, in terms of abundance of epiphytic algae, diatoms, or fungi. In contrast, larger and reproductively mature individuals that are not so severely limited by physiological constraints may increase their likelihood of mating by foraging higher in the understory.

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