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Avoidance of Canopy Gaps by a Common Land Snail, *Caracolus caracolla* (L.), in Montane Forest in Puerto Rico

Christopher P. Bloch^{1,*} and Michael Stock²

Abstract - Because canopy gaps are characterized by elevated temperature and decreased humidity relative to closed-canopy forest, terrestrial gastropods may be exposed to greater desiccation stress in gaps than in undisturbed forest. We placed individuals of *Caracolus caracolla* at the edges of canopy gaps in montane forest in Puerto Rico and observed their movements. Individuals preferentially moved out of gaps except in one gap on the first night of the study, and the proportion of individuals recaptured inside gaps decreased over time. Individuals moved, on average, farther into forest than into gaps. Juveniles and adults responded similarly. These results suggest that *C. caracolla* actively avoids canopy gaps, and that its activity and ability to disperse are restricted in a post-disturbance environment.

Introduction

Extensive research indicates that canopy gaps in tropical forests play a major role in the maintenance of high plant biodiversity (Brokaw and Busing 2000, Denslow 1987, Schnitzer and Carson 2001). Disturbances that produce canopy openings generate spatial heterogeneity in habitat structure and environmental conditions, and this heterogeneity often promotes high biodiversity of other taxa as well (i.e., the habitat heterogeneity hypothesis; MacArthur and MacArthur 1961, Rosenzweig 1995). Nevertheless, the effects of such heterogeneity likely differ depending on spatial scale and how different taxa respond to structural components of their environments (Wichmann et al. 2004).

Canopy openings may be of particular importance to the abundance and distribution of terrestrial gastropods. Many studies of responses of terrestrial gastropods to disturbance cite changes in microclimatic conditions (i.e., temperature and moisture) as important drivers of spatio-temporal patterns of abundance and biodiversity (e.g., Bloch and Willig 2006, Bloch et al. 2007, Hylander et al. 2004, Schilthuizen et al. 2005, Willig et al. 2007). This is unsurprising, as gastropods are restricted in range and activity by environmental conditions, more so than many other taxa. Canopy gaps exhibit higher daytime temperatures, lower humidity, and greater light intensity than do areas under intact canopy (Denslow 1980, Fernandez and Fetcher 1991), and the degree of difference increases with the size of the canopy opening (Lee 1978). These conditions are stressful for gastropods. Desiccation has been documented as a major source of mortality, especially for eggs and hatchlings (Heatwole and Heatwole 1978, Pollard 1975, Riddle 1983, Solem 1984). Moreover, movement is costly in terms of water, so individuals reduce their activity in hot, dry conditions (reviewed

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in Cook 2001). Microclimate therefore helps to explain both the well-documented tendency for terrestrial gastropods to restrict their movements to favorable habitats (e.g., Arnaud 2003, Baur 1986, Baur and Baur 1992) and the reduction of population size in a post-disturbance environment (Willig and Camilo 1991).

Despite the clear importance of microclimate, other factors may contribute strongly to responses of gastropods to disturbance. In addition to changing microclimatic conditions, the formation of a canopy opening has multiple effects. Biomass is translocated from the canopy to the forest floor, potentially increasing the availability of resources. In addition, treefalls and subsequent secondary succession alter vegetation structure and composition. Dense, structurally complex vegetation, such as would be expected during succession in a canopy gap, can provide refugia, reducing susceptibility to predation (e.g., Bennetts et al. 2006, Gause 1934, Warfe and Barmuta 2004) or unfavorable environmental conditions (Hylander et al. 2004). Thus, the overriding importance of climatic conditions in gaps as a driver of abundance and biodiversity of gastropods is questionable, especially in forests in the Caribbean Basin, where the gastropod fauna has experienced hurricanes, treefalls, and landslides throughout its evolution.

Alvarez and Willig (1993) demonstrated differences in abundances of several species of snails between canopy gaps and intact forest in the Luquillo Mountains of northeastern Puerto Rico. For example, *Caracolus caracolla* (L.), one of the most abundant (Bloch and Willig 2009, Willig et al. 1998) and most intensively studied terrestrial gastropods in the Luquillo Mountains, is found at significantly lower densities in gaps than under intact canopy (Alvarez and Willig 1993). It remains unclear, however, the reason for these differences (e.g., avoidance of gaps or in situ mortality in gaps).

To investigate the behavior of *C. caracolla* with respect to canopy gaps, we conducted a short-term experiment in which we experimentally placed snails at the edges of canopy gaps in a subtropical wet forest in the Luquillo Mountains and then observed their movements. We hypothesized that snails would (1) move with greater frequency away from canopy gaps than into them, and (2) would move greater distances away from gaps than into them. Smaller individuals should be more constrained by temperature and desiccation stress (Heatwole and Heatwole 1978) as a consequence of greater surface area-to-volume ratios, and juvenile snails often disperse greater distances than do adults (e.g., Tomiyama and Nakane 1993). Therefore, we further hypothesized that smaller individuals would move, on average, further from gap edges than would larger individuals.

Methods

Study site and organism

The Luquillo Experimental Forest (LEF) comprises 11,300 ha in the Luquillo Mountains. This study occurred in tabonuco forest, a subtropical wet forest type (Ewel and Whitmore 1973) found in the LEF at elevations up to approximately 600 m. This forest type derives its name from the vernacular name of the dominant hardwood, *Dacryodes excelsa* Vahl (Tabonuco) (Burseraceae), although

other species (e.g., *Manilkara bidentata* (A. DC) A. Chev. [Balatá or Ausubo or Massaranduba], *Sloanea berteriana* Choisy ex DC [Montillo or Bullwood], *Guarea guidonia* (L.) Sleumer (Requia or Trompillo or Guaraguao or American Muskwood), and *Prestoea acuminata* var. *montana* (Graham) A. Hend. & G. Galeano [Sierran Palm]) are also common in the canopy (Lawrence 1996). Precipitation is substantial, averaging over 300 cm per year (García-Martinó et al. 1996, Heartsill-Scalley et al. 2007). A modestly drier period typically extends from January to April, with March being the driest month of the year (Heartsill-Scalley et al. 2007). The present study was conducted in July, a month with an average precipitation of approximately 9.25 mm per day (Heartsill-Scalley et al. 2007). Humidity remains consistently high, and temperature exhibits relatively little seasonal or diurnal variation (Odum et al. 1970). The Luquillo Mountains experience a major hurricane (category 3 or greater on the Saffir-Simpson scale) every 50 to 60 years on average (Scatena and Larsen 1991), although only 9 years separated the two most recent major hurricanes (Hugo in 1989 and Georges in 1998). These large-scale disturbances dramatically alter biotic and abiotic conditions by damaging or defoliating trees, producing extensive runoff, and generating additional disturbances such as landslides (Brokaw et al. 2012). After a major hurricane, canopy cover regenerates to pre-hurricane levels within approximately 5–10 years (Brokaw et al. 2012), although disturbance of the soil by subsequent large landslides results in much longer recovery times (Guariguata 1990). Background mortality of 2–5% of trees in the LEF per year (Lugo and Waide 1993) produces smaller-scale canopy gaps from individual treefalls. The time necessary for canopy closure varies depending on the size of the gap, but generally is less than that needed for closure of large gaps caused by hurricanes or landslides.

Caracolus caracolla is a large (shell diameter up to 65 mm; Heatwole and Heatwole 1978) and long-lived (up to 15 years; M.R. Willig, University of Connecticut, Storrs, CT, USA, and C.P. Bloch, unpubl. data) snail species in the LEF. It is found in habitats throughout most of Puerto Rico (van der Schalie 1948), but attains its highest densities in mesic montane forests (Heatwole and Heatwole 1978). It is largely arboreal, but uses other habitats (e.g., leaf litter, rocks) readily, and is found more commonly in the leaf litter under drier conditions (Heatwole and Heatwole 1978). Juveniles typically occupy cooler, wetter, and less-exposed microsites than do adults (Heatwole and Heatwole 1978). *Caracolus caracolla* is euryphagic, having a diet that includes live and dead leaves from both monocots and dicots, fruits, seeds, fungi, and diatoms (Garrison and Willig 1996, Heatwole and Heatwole 1978). The biology of *C. caracolla* is well described, the species is abundant enough to collect in large numbers, and individuals are large enough to mark with unique tags (Bloch and Willig 2009, Willig et al. 1998). Therefore, it is an ideal organism for use in a study such as this one.

Field methodology

Three canopy gaps were located in tabonuco forest near El Verde Field Station (18°19'16.63"N, 65°49'11.26"W). Gaps conformed to the definition of Brokaw

(1982); they were vertical openings in the forest that extended through all levels of vegetation at least down to 2 m from the forest floor. Area of each gap exceeded 150 m² (ranging from approximately 160–200 m²). *Caracolus caracolla* is uncommon in areas that have steep slopes (Heatwole and Heatwole 1978), so gaps on steep slopes were not used. To evaluate structural complexity of habitats, species-specific apparency of vegetation was estimated at two locations in each gap (2 m from the northern edge and 2 m from the southern edge), as well as at two locations in the forest matrix surrounding each gap (again, 2 m from the northern edge and 2 m from the southern edge). Apparency was measured as the number of intercepts of each species (or rocks or dead plant matter) on a plant apparency device (Secretst et al. 1996), a 3-m tall pole with four 0.5-m wooden dowels positioned at 90° to each other at each of 7 heights (0.0, 0.5, 1.0, 1.5, 2.0, 2.5, and 3.0 m). Thus, apparency is a measure of 3-dimensional structure of vegetation, not a count of individuals.

One hundred-twenty individuals of *C. caracolla* were collected from the grounds of El Verde Field Station and surrounding tabonuco forest, such that no gap was near the home range of any collected individual. Each individual was measured to the nearest 0.1 mm with dial calipers and uniquely marked by affixing a numbered plastic tag to the shell with super glue. Snails were divided into six groups of 20, each representing a range of body size (i.e., shell diameter) from approximately 25 mm to 60 mm. Two of these groups were randomly assigned to each of the three canopy gaps, one to the northern boundary and one to the southern boundary. The next day (22 July 2010), in late afternoon (16:00–18:00), each group of 20 snails was placed at the edge of its assigned canopy gap. Snails were placed at the edge of gaps rather than in the center to provide them with the option of moving either into or away from the gaps. In each case, the 20 individuals were spaced evenly along an 8-m transect that followed the edge of the gap. The order of individuals along each transect was randomly determined.

One, three, and seven days after snails were placed at gaps, we recorded their locations. Two researchers spent a minimum of 30 minutes searching for snails in the area around each transect, attempting to find as many marked snails as possible without causing excessive trampling or disturbance of habitat. One researcher searched inside the gap, while the other searched in the forest matrix outside the gap (these roles were assigned randomly for each transect on each night). We recorded location and distance moved for each snail found. All sampling was conducted at night (after 19:00) to coincide with peak snail activity (Heatwole and Heatwole 1978, Willig et al. 1998) and maximize the likelihood of capture.

Statistical analysis

Analysis of variance (ANOVA) was used to test for differences in habitat structure (defined as height-specific apparency of rocks and live or dead vegetation) and also to test for differences in apparency of live plants only. In both cases, there were two factors of interest: habitat type (i.e., whether the sample was taken in the gap or the forest matrix) and the height at which apparency was measured. The identity of the gap being sampled was modelled as a random (Model II) factor. A

repeated-measures ANOVA was used to compare species richness between gaps and associated forest.

Hierarchical loglinear analysis was used to compare the frequency with which snails were observed in gaps versus forest. The analysis first produced a saturated model including the factors gap identity, transect (north or south), day of sampling, habitat type (i.e., gap or forest), and their interactions. Because this model included all of the variables, it fit the data exactly. The analysis proceeded by producing an unsaturated model by removing first the highest-order effect (i.e., the four-way interaction) and evaluating whether this produced a significant change in model fit. Subsequent models progressively removed third-order effects, second-order effects, and main effects. If removing effects of a particular order resulted in a significant change in model fit, partial chi-square associations were used to identify which effects of that order were significantly associated with differences in frequency of snails. For this analysis, snails that remained in place at the edge of the gap were considered to be inside the gap.

To test whether distance and direction of movement by snails by the seventh day depended on body size, a single-factor analysis of covariance was used, with shell diameter as the covariate and gap identity modeled as a random (Model II) factor. The analysis was run twice. First, to account for differences in direction of movement, distance moved into a gap was coded as a negative number, whereas distance moved out of a gap was coded as a positive number. Second, the analysis was run using absolute distances moved, without reference to direction of movement.

Statistical analyses were conducted using SPSS v. 18 software. Significance was assessed at a confidence level of $\alpha = 0.05$. All analyses are described in detail in Sokal and Rohlf (2012).

Results

Of the plant taxa observed at the three sites (the most abundant of which are listed in Table 1), only a grass, *Ichnanthus pallens*, was consistently found in greater abundance in gaps than in surrounding forest matrix (hereafter, forest). No species was consistently found in greater abundance in forest than in gaps, and none was found exclusively in one habitat or the other. Species richness of live plants sampled did not differ significantly between gaps (5.2 ± 2.2 [standard deviation]) and forest (4.2 ± 2.1), although this difference approached significance ($F = 6.40$; $df = 1,3$; $P = 0.085$).

Because differences in species composition were not clear between gaps and forest, analyses focused on structural complexity of habitats. Differences in habitat structure (measured as apparency of live vegetation, dead vegetation, and rocks) depended on the height at which apparency was measured (significant habitat by height interaction; Table 2). Specifically, apparency was greater in gaps than in forest at 0 m, but greater in forest than in gaps at 1 m and above. The same pattern was evident if dead vegetation and rocks were excluded from analyses to focus on live plants, except that the rate of decrease in apparency with increasing height was lower.

On any particular night of the study, the proportion of snails recaptured at any particular gap ranged from 0.28 to 0.55. Over the course of the entire study, the

Table 1. Common plant taxa observed in canopy gaps and adjacent forest matrix, primary life form of each, and rank apparency in each habitat (1 = greatest, with *t* indicating a tie). Apparency is defined as the number of times a plant intercepts the plant apparency device (a 3-m pole with four 0.5-m wooden dowels set at 90° angles to each other, at each 0.5 m of height from ground level to 3 m; Secrest et al. 1996). Thus, apparency is a measure of foliar volume, rather than a count of individuals.

Species	Family	Life form	Rank in	
			Gaps	Forest
<i>Heliconia caribaea</i> (Lamarck) (Lobsterclaw)	Heliconiaceae	Herb	5	3
<i>Ichnanthus pallens</i> (Swartz) Munro ex Benth. (Caruzo)	Poaceae	Grass	1	4
<i>Marcgravia</i> spp.	Marcgraviaceae	Liana	13 <i>t</i>	9
<i>Palicourea croceoides</i> Ham. (Yellow-cedar) (= <i>Palicourea riparia</i> Benth.)	Rubiaceae	Shrub	7	7 <i>t</i>
<i>Philodendron</i> spp.	Araceae	Liana	9 <i>t</i>	7 <i>t</i>
<i>Piper glabrescens</i> (Miquel) C. DC. (Guyanese Pepper)	Piperaceae	Shrub	6	10 <i>t</i>
<i>Piper hispidum</i> Sw. (Jamaican Pepper)	Piperaceae	Shrub	13 <i>t</i>	12 <i>t</i>
<i>Prestoea acuminata</i> var. <i>montana</i> (Graham) (Sierra Palm)	Arecaceae	Palm	2	1
<i>Psychogria berteriana</i> DC. (Cachimbo-cumun) (= <i>Psychotria berteriana</i> DC.)	Rubiaceae	Shrub	8	5
<i>Rourea surinamensis</i> Miquel (Juan Caliente)	Connaraceae	Liana	11	6
<i>Sloanea berteriana</i> Choisy ex DC. (Bullwood) (= <i>Sloanea berteriana</i> Choisy)	Eleaeocarpaceae	Tree	12	12 <i>t</i>
<i>Miconia</i> spp.	Melastomataceae	Shrub	4	10 <i>t</i>
Unidentified	Rubiaceae	Shrub	9 <i>t</i>	12 <i>t</i>
Various Pteridophytes	Various	Fern	3	2

Table 2. Results of analysis of variance to compare habitat complexity among heights from 0–3 m and between canopy gaps and surrounding forest (Habitat). Error degrees of freedom (df) and error sums of squares are not identical among model terms because gap identity (Gap) was modeled as a random (Model II) factor.

Term	Source	Sum of squares	df	Mean square	<i>F</i>	<i>P</i>
Gap	Hypothesis	37.17	2	18.58	1.10	0.404
	Error	82.67	5	16.92		
Height	Hypothesis	7411.45	6	1235.24	55.04	<0.001
	Error	269.33	12	22.44		
Habitat	Hypothesis	51.86	1	51.86	12.41	0.072
	Error	8.36	2	4.18		
Height × Gap	Hypothesis	269.33	12	22.44	2.31	0.080
	Error	116.48	12	9.71		
Habitat × Gap	Hypothesis	8.36	2	4.18	0.43	0.660
	Error	116.48	12	9.71		
Habitat × Height	Hypothesis	1085.31	6	180.89	18.64	<0.001
	Error	116.48	12	9.71		
Height × Gap × Habitat	Hypothesis	116.48	12	9.71	0.59	0.841
	Error	696.00	42	16.57		

proportion of individuals recaptured was 0.73 (87 of 120 individuals). The remaining 33 individuals were never located.

Hierarchical log-linear analysis of snail distributions revealed significant third-order (likelihood ratio $\chi^2 = 21.06$, $df = 12$, $P = 0.049$), second-order ($\chi^2 = 32.05$, $df = 13$, $P = 0.002$), and first-order ($\chi^2 = 116.65$, $df = 35$, $P < 0.001$) effects. Specifically, factors that significantly affected model fit were habitat (gap versus forest), its two-way interactions with sampling day and gap identity, and the 3-way interaction among habitat, day, and gap identity (Table 3). This 3-way interaction indicated that although snails were more frequently observed in forest than in gaps overall, this effect was not consistent among sites and nights. At one site, most snails (14 of 15) were found in the gap on the first night, whereas most snails were found in the forest at the other sites and on the remaining nights of sampling at all three sites.

Body size of snails did not affect direction and distance of movement. Analysis of covariance revealed no significant effect of shell diameter on movement when direction of movement was included in the analysis ($F = 0.08$; $df = 1, 41$; $P = 0.775$) or when direction of movement was discounted ($F = 0.07$; $df = 1, 41$; $P = 0.792$). These results were nearly identical because most snails (38 of 45) observed on the final day of sampling had moved in the same direction (out of the gaps), and 3 of the remaining 7 individuals were observed at the same location where they were placed at the beginning of the experiment. Of the individuals that were found the last night in or on the edge of the gap, all were adults or large subadults (the smallest was 37.5 mm in diameter). The maximum observed distance a snail moved into a gap was 1.6 m (a 50.5-mm adult), whereas 21 individuals exceeded 1.6 m of movement into the forest (maximum: 8.6 m). Mean movement into gaps was 0.67 ± 0.67 m ($n = 4$, excluding individuals that did not move), and mean movement into forest was 2.03

Table 3. Results of hierarchical loglinear analysis to investigate frequency of occurrence of *Caracolus caracolla* experimentally placed on edges of canopy gaps and then observed on subsequent nights. Factors of interest were gap identity (Gap), whether the snail was on the north or south side of the gap (Transect), habitat in which the snail was found (in the gap or under forest canopy; Habitat), day of sampling (Day), and all possible interactions.

Effect	Partial χ^2	df	P
Gap \times Transect \times Habitat \times Day	7.17	4	0.127
Gap \times Transect \times Habitat	0.28	2	0.870
Gap \times Transect \times Day	3.04	4	0.551
Gap \times Habitat \times Day	17.61	4	0.001
Transect \times Habitat \times Day	1.61	2	0.447
Gap \times Transect	3.62	2	0.164
Gap \times Habitat	13.97	2	0.001
Transect \times Habitat	0.99	1	0.320
Gap \times Day	2.92	4	0.572
Transect \times Day	1.49	2	0.475
Habitat \times Day	14.39	2	0.001
Gap	3.68	2	0.159
Transect	0.33	1	0.566
Habitat	51.54	1	<0.001
Day	0.82	2	0.663

± 1.63 m ($n = 38$). All snails observed on the final night of the study were still alive, including those that had not moved from where they were originally placed.

Discussion

Previous studies demonstrated that snails avoid moving through unsuitable habitat (Arnaud 2003, Baur 1986, A. Baur and B. Baur 1992, B. Baur and A. Baur 1995, Hall and Hadfield 2009). Indeed, terrestrial gastropods become restricted to habitat “islands” far more easily than other taxa that are more vagile or less dependent on environmental conditions (Gittenberger 2007). In addition, many snail species reduce activity during dry conditions (Bailey 1975, Cook 2001, Pollard 1975) or actively avoid intense light by burrowing (Gelderloos 1979). Although the results of a field study of such short duration as ours must be considered preliminary, the response of *C. caracolla* to canopy gaps was consistent with these previous observations.

Individuals of *C. caracolla* moved preferentially out of canopy gaps and moved farther into closed-canopy forest than into gaps. The only exception was in a single gap on the first day after placement of snails on transects. If canopy gaps represent harsh environmental conditions, such that *C. caracolla* generally avoids movement through them, this exception was likely a function of precipitation and cloud cover; rainfall was quite heavy in the week leading up to the study (421.6 mm, including 50.8 mm on the day snails were placed on transects) and lower during the study (69.1 mm; data from the Luquillo Mountains Long-Term Ecological Research Program, available at <http://luq.lternet.edu/data/luqmetadata14>). This finding suggests that, even though the overall climate of tabonuco forest is generally benign for snails, with consistently high precipitation and humidity (Heartsill-Scalley et al. 2007, Odum et al. 1970), *C. caracolla* avoids canopy gaps except during unusually cool and wet conditions.

Gaps receive significantly more direct sunlight than does forest understory, but the degree of difference changes among months, being greatest in the summer and least during the winter (Marthews et al. 2008) because of changing solar angle. Strong responses of *C. caracolla* to canopy gaps were observed in late July. In northeastern Puerto Rico, although sunlight is most direct and intense during the summer, rainfall (and thus cloud cover) is also frequent and heavy then (Heartsill-Scalley et al. 2007). Changes in intensity of sunlight and frequency of rainfall at other times of year might mediate responses of *C. caracolla* to canopy gaps. However, in areas of open canopy, periods of high light intensity are common throughout the year (Fernandez and Fetcher 1991). Consequently, the tendency of *C. caracolla* to move away from gaps probably strengthens during the dry season (January through April).

The results were strong and consistent even though we tested responses of snails only to individual treefall gaps. Larger-scale disturbances, such as hurricanes, probably strengthen the response of *C. caracolla* to canopy gaps. Hurricane Hugo (September 1989), for example, was especially severe. This storm caused large and widespread canopy openings, killing approximately 25% and completely defoliating over 50% of trees in the Luquillo Forest Dynamics Plot (Zimmerman et al.

1994), a 16-ha area that is located near the canopy gaps we observed in the present study. Moreover, Hurricane Hugo was followed by a 3-month drought (Waide 1991). The extended dry weather almost certainly intensified the pressure on snails to avoid canopy gaps, and contributed to an extreme reduction in gastropod abundance (Willig and Camilo 1991).

Habitat complexity at ground level was greater in gaps than in forest. Snails often prefer complex habitats, ostensibly because they provide shelter from predators or environmental stress (e.g., Perea et al. 2007). In the present study, however, *C. caracolla* more frequently moved toward the less structurally complex habitat. Most likely, light intensity or associated microclimatic conditions induce stronger responses than does habitat complexity, at least at ground level. It is unknown whether *C. caracolla* responds to light intensity per se or some other associated environmental cue, but the species is most active at night and on cloudy days (Heatwole and Heatwole 1978), which is consistent with our observation that it prefers closed canopy over gaps and the hypothesis that it avoids gaps to reduce exposure to heat and sunlight. Also, *C. caracolla* prefers larger trees over smaller trees as a substrate (Heatwole and Heatwole 1978), and taller vegetation may provide important resources that are unavailable near ground level, where most vegetation exists in gaps. Taller vegetation may also provide a more effective refuge from some predators, such as the semiterrestrial crab *Epilobocera sinuatifrons* (Milne-Edwards) (Buruquena), which, under wet conditions, forages on land and preys upon terrestrial invertebrates (Covich and McDowell 1996, March and Pringle 2003), including snails (C.P. Bloch, pers. observ.).

Two constraints to experimental design conceivably could have influenced the outcome of the experiment. First, even if snails were moving at random, more would be expected to enter forest than gaps simply because the area of forest is greater than that of the gaps. Second, crowding may affect both activity and growth rates of some snail species (Cameron and Carter 1979, Jess and Marks 1995), and the close proximity of other individuals along the transects may have affected movement rate or direction for *C. caracolla*. Neither of these scenarios, however, is a likely explanation for our results. We guarded against the area effect by limiting our searches to the north and south sides of the gaps, parallel to our transects, and only one individual was recaptured at a greater distance into the forest (8.6 m) than was possible in the opposite direction. Therefore, although there might have been an area effect, the difference in area sampled between forest and gap is insufficient to explain the strength of the response of *C. caracolla* (i.e., only 4 of 45 individuals recaptured on the last day of sampling were found farther into the gap than where they were initially placed). Crowding is also unlikely to have affected our results. Most studies of crowding cite chemical cues in mucus as a probable mechanism for inhibition of growth or activity (Cook 2001), but few, if any, mucus trails should have been present at the outset of this experiment, as individuals were placed on the transects by hand. Moreover, crowding effects are probably much less prevalent in the field than in laboratory colonies (Baur 1993). Indeed, *C. caracolla* aggregates at favorable sites, with individuals often passing inactive periods in direct physical contact with one another (Heatwole and Heatwole 1978), and intraspecific

competition seems to have little effect on growth rates of individuals in the field (Bloch and Willig 2009).

Recent long-term studies (Bloch et al. 2007, Willig et al. 2007) argue that the large, widespread canopy openings generated by hurricanes may restrict the dispersal of gastropods by rendering large areas of forest inhospitable, and that this dispersal limitation influences spatial and temporal patterns of gastropod biodiversity as the canopy recovers over time after disturbance. Our current results are consistent with this hypothesis, though this study was not a conclusive test. Population-level responses of gastropods in the Luquillo Mountains to disturbance are species-specific. For example, although some species (including *C. caracolla*) are found in greater numbers in forest than in gaps, others are observed in greater abundance in gaps (Alvarez and Willig 1993). Moreover, responses may differ between disturbance types. For example, abundance of *Nenia tridens* (Schweigger), another abundant snail in the Luquillo Mountains, is greater in treefall gaps than in surrounding forest (Alvarez and Willig 1993), but this species was among those that experienced the most dramatic declines after Hurricanes Hugo and Georges (Bloch and Willig 2006, Willig and Camilo 1991), suggesting that the size and spatial configuration of canopy openings influence species responses. Particularly severe hurricanes may produce canopy openings of sufficient number, size, and proximity to negatively affect even species that tolerate conditions in smaller gaps. Clearly, additional studies will be necessary to facilitate generalizations of our results to other species or among disturbance events.

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