

POPULATION DYNAMICS AND NATURAL HISTORY OF A  
NEOTROPICAL WALKING STICK, *LAMPONIOUS PORTORICENSIS*  
REHN (PHASMATODEA: PHASMATIDAE)

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**ABSTRACT.**—Although phasmatids are conspicuous components of many neotropical ecosystems, their biology and natural history are poorly understood. Herein, the population structure and movement patterns of the endemic Puerto Rican walking stick, *Lamponius portoricensis*, are described based on mark-recapture methods. Individuals were marked and observed over two three-week periods in the wet season. Individuals moved an average of only 0.55 meters per day; significant differences between phases for movement parameters were not obtained. The greatest individual movement was 6.02 meters in two days. A significant shift in size (=age) structure occurred between experimental phases and was attributable to the higher proportion of short Phase I nymphs (10.1-30.0 mm) and a higher proportion large Phase II specimens (30.1-110.0 mm). The spatial distribution of captures was significantly different than random; the observed clumped distribution of recaptures probably was affected by the non-random distribution of forage plants within the study area. All captures were obtained in the understory ( $\leq 1.3$  meter); most frequently used forage plants included *Piper treleaseanum*, *Dendropanax arboreus*, *Piper hispidum*, and *Urera baccifera*. Predation escape mechanisms and demographic strategies in *L. portoricensis* are discussed in relation to habitat preference. *Key words:* *Lamponius*; phasmatid; demography; Puerto Rico; population ecology.

Detailed studies of neotropical insect population ecology have lagged far behind similar studies on temperate zone species. The poor and often chaotic state of neotropical insect taxonomy, as well as the dearth of insect ecologists working in Latin America have contributed to the imbroglío. Although many papers provided descriptions of the natural history and ecology of tropical taxa (for example, Collenette and Talbot, 1928; Corn, 1972; Young, 1972, 1973, 1982; Muyschondt, 1973a, 1973b; Palmer, 1976; Sivinski, 1978, 1980), fewer quantitative studies have been conducted (for example, Benson and Emel, 1973; Freeman, 1973, 1980; Freeman and Taffe, 1974; Freeman and Jayasingh, 1975; Wolda, 1978a, 1978b, 1979a, 1979b, 1980a, 1980b, 1983; Jayasingh and Freeman, 1980; Wolda and Galindo, 1981) and these have not considered movement dynamics in addition to density and home range parameters. Turner (1971), Ehrlich and Gilbert (1973), and Cook et al. (1976) provided notable exceptions for butterflies. Studies that involved the passive capture of specimens in insect traps (Penny and Arias, 1981) are valuable, but provide minimum population estimates and, unless traps are checked daily, cannot be used to monitor diel patterns of population density.

Moreover, movement and dispersal data cannot be obtained because captured individuals are permanently removed from the population.

The Phasmatodea, or walking sticks, are primarily a tropical group of herbivores that occasionally have an economic impact on human-manipulated systems (Campbell, 1960, 1961, 1966, 1974; Mazenac, 1966, 1967, 1968; Campbell and Hadlington, 1967; Paine, 1968). Many species are large but cryptic because of their resemblance to twigs. The biology of Phasmatidae is poorly known; the work of Bedford (1978) is the best contemporary review. The only quantitative study on this group estimated population densities of two species in southeastern Australia that occasionally reach plague numbers in *Eucalyptus* forests (Campbell, 1960). By sampling egg density and frass production from nymphs and adults at various forest sites, future magnitudes of infestation could be estimated. The ecological or population data reported for all neotropical species is entirely descriptive (Robinson, 1968a, 1968b, 1969; Moxey, 1971) or anecdotal (Wolcott, 1948).

Since 1981, various animal components of an insular neotropical rain forest in eastern Puerto Rico have been studied as part of an investigation with the goal of constructing a comprehensive food web for the community. This work has been funded by the U.S. Department of Energy as part of an ongoing study of nutrient cycling. The phasmatid, *Lamponius portoricensis* Rehn, is a large (up to 110 mm), common insect in Puerto Rico and is a potentially important grazer in the forest understory. Most published works on this species are systematic (for references see Moxey, 1971, 1972), although limited comments on natural history are included also. The purpose of this study is to describe the population dynamics of a tropical phasmatid during two portions of the wet season, including data on individual movements, daily population size, size (=age) class structure, and other ecological attributes of the species. To our knowledge, this is the first investigation to apply mark-recapture methodologies to a population of phasmatids.

#### DESCRIPTION OF THE STUDY SITE AND METHODS

Field work was conducted during the summer of 1982 at El Verde Field Station (latitude 18° 19' N, longitude 65° 45' W), located on the west slope of the Luquillo Mountains in eastern Puerto Rico. This site is classified as a subtropical rainforest (Holdridge, 1947; Ewel and Whitmore, 1973) and annually receives an average of 3456 mm of rainfall. Tabonuco (*Dacryodes excelsa*) is the dominant hardwood; other common trees include *Buchenavia capitata*, *Inga fagifolia*, *Guarea trichilioides*, and *Prestoea montana*. *Lamponius portoricensis* is a common inhabitant of the forest, where it is especially abundant in open or disturbed areas of the understory. It is polyphagous and feeds on *Dendropanax arboreus*, *Piper hispidum*, *P. treleaseanum*, and *Urera baccifera*, shrubs that commonly occur in exposed areas (Willig, unpublished data). Walking sticks are active at night, during which time they feed and engage in sexual activities. Two other phasmatids, *Diapherodes achalus* (Rehn) and *Agamemnon iphimedia* Moxey, occur at the site, but they are quite rare and are not further discussed in this report.

The study comprised two mark-recapture periods: Phase I occurred during a dry period of the wet season from 17 June to 4 July 1982, and Phase II was conducted from 10 July to 1 August 1982 when precipitation was more characteristic of the wet season. Exceptionally high precipitation precluded field work on three nights during Phase I and two nights during Phase II. The study site, contained within a light gap zone of the forest, encompassed a grid of 10 by 10 meters consisting of 100 square meter quadrats. Early successional plants dominated the understory and included *P. treleaseanum*, *P. hispidum*, *U. baccifera*, *D. arboreus*, *Ruella coccinea*, *Inga vera*, and *Heliconius* sp. Because shrubs did not exceed a height of four meters, it was possible to meticulously examine all portions of each plant during each sampling period. Sampling occurred between 1930 and 0230 hours; unmarked insects were marked with a unique number on the dorsum or venter (or both) of the thorax using a Pilot permanent ink felt-tipped pen before being released at the site of capture. In addition, we recorded length (mm), age-sex category (adult male, adult female, nymph), activity (moving, eating, resting, copulating), substrate type (ground, leaf surface, stem), quadrat location on the grid, and species of forage plant, when applicable, for each capture.

*Lamponius portoricensis* is sexually dimorphic in length (males:  $\bar{Y} = 80.6$  mm,  $s = 3.90$  mm,  $n = 20$ ; females:  $\bar{Y} = 89.6$  mm,  $s = 6.44$  mm,  $n = 20$ ) with the females significantly larger than the males—Behrns-Fisher *t*-test for samples with unequal variance:  $t' = 5.35$ ,  $P < .05$  (Snedecor and Cochran, 1967). Adults could be distinguished from nymphs by the extent of development of the terminal genitalia as well as by size. Adult males were at least 72 mm long and adult females were at least 77 mm long.

The techniques of Scott (1974, 1975) were used to analyze population movement parameters. Straight-line distances between temporally consecutive captures ( $d_i$ ) were summed ( $D_i = \sum d_i$ ) and divided by the total number of days between first and last capture ( $T_i$ ), yielding a velocity ( $V_i = D_i/T_i$ ). We calculated average  $D_i$ ,  $T_i$ , and  $V_i$  for each phase of the study. The length of a straight line between the most distant capture points for an individual was used to estimate its home range. Home range size would be expected to increase as recapture frequency increases, especially for home ranges determined from a low number of captures (Southwood, 1978; Mares et al., 1980). Frequently, however, few individuals are captured sufficiently often to produce a reliable estimate of home range and a compromise between number of individuals and number of captures per individual must be obtained in order to produce a gross estimate of home range. Brussard et al. (1974) calculated home ranges for the checkerspot butterfly, *Euphydryas editha*, using individuals with a minimum of five recaptures. Similarly, we restricted the calculation of  $R_{max}$  (home range size) to those individuals with five or more captures. Although the capture criterion is somewhat arbitrary, the lack of a significant correlation between  $R_{max}$  and capture number for individuals with five or more captures in Phase I ( $r = .49$ ,  $df = 14$ ,  $p > .05$ ) and Phase II ( $r = .32$ ,  $df = 16$ ,  $P > .05$ ) suggests that our decision is unbiased.

Comparisons of dispersion for Phases I and II were accomplished using Morisita's (1959) Index:

$$I\delta = \frac{\sum_{i=1}^q n_i(n_i-1)}{N(N-1)}$$

where  $q$  = number of quadrats,  $n_i$  = the number of individuals captured in quadrat  $i$ , and  $N$  = the total number of captures including all quadrats ( $\sum n_i$ ). The index is easy to calculate and provides a direct method of comparison when quadrat number is equal and  $n_i$  is relatively large. Values less than one indicate uniformity; values equal to one indicate randomness; and values greater than one indicate aggregation.

TABLE 1. Number of *L. portoricensis* marked (N), number recaptured (RC), percent recaptured (% RC), and average number of recaptures per individual (RCav).

Phase	Stage	Sex	N	RC	% RC	RCav
I	Adult	Male	13	4	31	0.92
		Female	3	2	67	2.67
	Nymph	—	108	58	54	1.32
II	Adult	Male	7	3	43	0.43
		Female	1	0	0	0.00
	Nymph	—	114	62	54	1.75
Totals	Phase I		124	64	56	1.31
	Phase II		122	65	53	1.66

We used the Bailey (1951, 1952), Jolly (1965), and Manly-Parr (1968) methods for estimating daily population size ( $\bar{N}_t$ ), survival or residency rates ( $\hat{\phi}_t$ ), proportion of the marked animals in the population ( $\hat{\alpha}_t$ ), and number of marked animals in the population ( $\hat{M}_t$ ). The latter two models are less deterministic than others (Seber, 1973; Southwood, 1978) and allow for daily ingress and egress. Further, the Manly-Parr model does not assume that mortality is independent of age. We marked both adults and nymphs, but if a marked nymph molted, it would be considered a new capture, and the previously marked individual would be considered lost to the population. As a result, both the Jolly and Manly-Parr demographic techniques probably produce somewhat high population estimates and artificially low residency rates. An additional complication arises because these models cannot distinguish between emmigration, death, and molting (that is, loss of marks); hence, we did not compute daily immigration-emmigration rates ( $\hat{b}_t$ ). In addition, the computation of average individual life spans, as done for damselflies by Garrison (1978) and Garrison and Hafernik (1981), is not applicable here.

Although the Bailey triple-catch method is less likely to accurately estimate the magnitude of population variation, it does act as a check on the biases of the other two methods because the effects of losing marked individuals through molting or death would be small over the three-day sample period of each estimate. If all three estimation techniques yield similar average population estimates, then one can assume that population estimates are reliable and robust with respect to deviations from their assumptions. Many phasmatid species are apparently long-lived—nine to 11 months for *Phyllium biculatum* Gray (Foucher, 1916a) three weeks to eight months for *Cyphoerania gigas* (Linnaeus) (Foucher, 1916b). One of us (Willig) maintained 20 adult *L. portoricensis* for 50 days before concluding a feeding experiment. As such, the use of mark-recapture data for the calculation of average life span ( $\hat{\phi}_t$ ) of *L. portoricensis* would be biased, yielding reduced rates of survivorship.

## RESULTS

One hundred twenty-four and 122 walking sticks were marked during Phases I and II, respectively (Table 1). Recapture statistics were similar in both phases: 56 percent of the marked individuals were recaptured during Phase I, and 53 percent of the marked individuals were recaptured during Phase II. In both phases, the majority of the captured individuals were nymphs (Table 1, Fig. 1); adult females were the least abundant component of the population. The number of recaptures per individual in adults ranged from zero for Phase II females to a high of 2.67 for

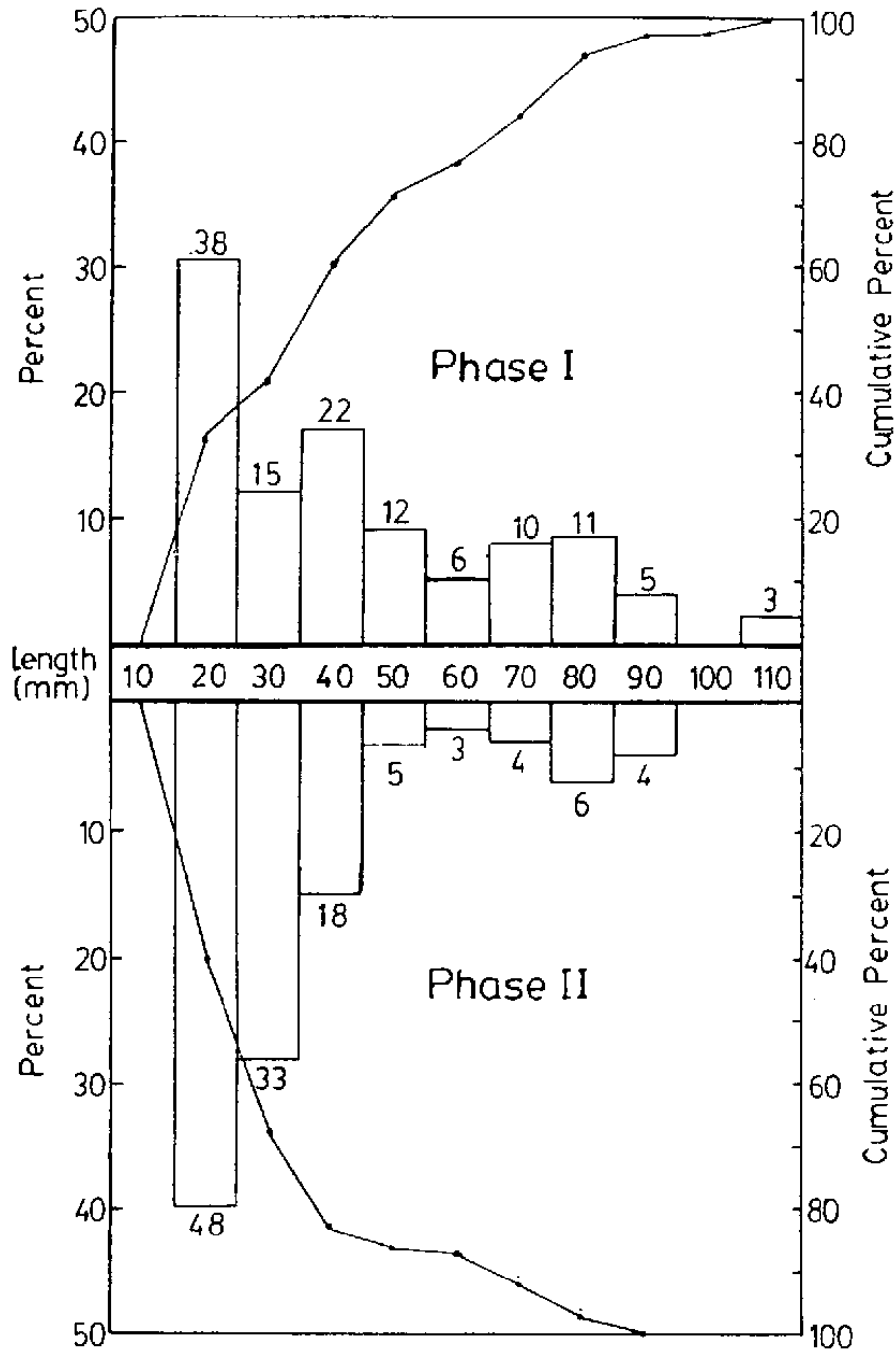


FIGURE I. Bar histogram indicating the size distribution of marked *L. portoricensis* population during Phase I and Phase II studies. Number above and below each histogram bar indicates sample size. Two individuals are not included in Phase I and Phase II because they were not measured. Cumulative percent of total population less than or equal to a particular size category is indicated by the superimposed graph. Length (mm) categories indicate 0.0-10.0 mm, 10.1-20.0 mm, and so on.

females in Phase I. Recapture data for nymphs were similar in both phases.

#### *Population Structure*

The size distribution of individuals was significantly different during Phases I and II (Fig. 1, Contingency Chi-Square Test:  $X^2 = 17.29$ ,  $df = 7$ ,  $0.025 > P > 0.01$ ). This difference was attributable to a higher proportion of short individuals (10.1-30.0 mm) in Phase II and a higher proportion of long individuals (30.1-110.0 mm) in Phase I. Between 5 and 16 July, a new cohort of hatchlings may have contributed to the smaller length categories in Phase II. Individuals shorter than 10.0 mm were not observed in either phase; these walking sticks were probably inconspicuous and/or occurred in an unsampled microhabitat (that is, beneath the leaf litter).

Mark-recapture studies inherently assume that marking does not alter an animal's behavior or recapturability relative to unmarked specimens. Coefficients of dispersion ( $CD = S^2/\bar{Y}$ ) for Phase I ( $CD = 2.21$ ) and Phase II ( $CD = 6.64$ ) were greater than one, indicating a contagious (aggregated) distribution—that is, compared to a stochastic distribution of recaptures ( $CD = 1.00$ ), more marked individuals than expected were never recaptured, and more marked specimens than expected were recaptured numerous times ( $\geq 5$ ). The distribution of recaptures among the marked population was compared to the binomial distribution in order to ascertain if the individuals in each phase exhibit equal catchability; the differences were highly significant in both phases ( $\chi^2$  test: Phase I— $X^2 = 79.78$ ,  $df = 3$ ,  $P < 0.001$ ; Phase II— $X^2 = 182.77$ ,  $df = 4$ ,  $P < 0.001$ ). Such unequal catchability may be attributed to: 1) different behavior in individual walking sticks (some may be inherent dispersers whereas others are residents); 2) a differential marking effect; or 3) a loss of marks after molting. Although marked and unmarked individuals enjoyed equal survivorship in the laboratory, all three factors probably contributed to the observed non-aleatory recapture phenomenon.

#### *Movements and Microhabitat*

In order to use the appropriate statistical test to detect mean differences between Phases I and II for  $T$  (days),  $D$  (meters),  $V$  (meters per day) and  $R_{max}$  (meters), we used the  $F_{max}$  test (Sokal and Rohlf, 1981) to evaluate the homogeneity of variances in Phases I and II for each parameter. Mean comparisons for parameters with homoscedastic variances were evaluated via a Student's  $t$ -test and those parameters with heteroscedastic variances were analyzed with a Behrens-Fisher  $t$ -test (Snedecor and Cochran, 1967). Significant differences did not exist between Phases I and II for any movement parameter. Walking sticks were generally philopatric, moving an average of only .55 meters per day.

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### Population Size

Demographic data for Phase I and Phase II are shown in Tables 3 and 4 respectively. The  $\hat{\alpha}_i$  values of Jolly generally exceeded 50 percent by the fourth sampling period and attained a maximum of 94 percent on 29 June. Daily residency rates determined by either the Jolly or Manly-Parr methods fluctuated greatly during both phases. Many values were greater than 1 and are biologically meaningless. Daily estimates of population size ( $\hat{N} \pm 1.96 \text{ SE}$ ) using the Bailey, Jolly, and Manly-Parr methods are in close agreement for both phases (Figs. 2 and 3). Compared to the Jolly method, the Manly-Parr method usually yielded slightly lower mean population size estimates. The majority of the daily population estimates were between 40 and 100 individuals (Figs. 2 and 3). Higher daily estimates (for example, 30 June, 16 July) had greater standard errors. Despite the shift in individual size distribution between phases (Fig. 1), the daily population estimates remained similar in both sampling periods.

Given the variation of daily population estimates, all three methods yielded similar mean results. Mean phase I population density estimates from the Bailey, Manly-Parr, and Jolly methods were 35.2 ( $S = 18.2$ ), 55.9 ( $S = 16.4$ ), and 64.6 ( $S = 24.4$ ) respectively. Mean phase II estimates of population density were 56.5 ( $S = 40.5$ ), 56.5 ( $S = 28.0$ ), and 63.3 ( $S = 35.0$ ) for the Bailey, Manly-Parr, and Jolly techniques respectively.

### Predators

We did not observe predatory encounters involving *L. portoricensis*; however, four ceratopogonids (Diptera) were feeding on a single 80 mm female on 24 June. Walking sticks were occasionally consumed by frogs (*Eleutherodactylus coqui*) and lizards (*Anolis cuvieri*, *A. evermanni*) based on stomach content analysis of those vertebrates.

## DISCUSSION

*Lamponius portoricensis* appears to be an important component of the Tabonuco forest ecosystem because of its association with light-gap formations. The importance of light gaps to floral succession and resilience in climatic climax forests has been stressed by many authors (Watt, 1947; Bray, 1956; Schulz, 1960; Taylor, 1962; Trimble and Tyron, 1966; Loucks, 1970; Mabberley, 1983; Wales, 1972; Whitmore, 1975, 1978; Hartshorn, 1978; Denslow, 1980; Wallace and Dunn, 1980), yet little attention has been focused on light-gap fauna. With the possible exception of certain gastropods (for example, *Caricola*), *L. portoricensis* appears to be a dominant light-gap herbivore based upon local population density and the size of the constituent individuals. It is not uncommon to see entire forage plants denuded as a result of the activities of *L. portoricensis*. One preferred food, *Urera baccifera*, acts as an effective nutrient sink for a variety of elements including P, Mn<sup>+++</sup>, K<sup>+</sup>,



TABLE 3. Population parameters estimated from multiple recapture data for *L. portoricensis* during Phase I:  $\hat{\alpha}_i$  = proportion of marked individuals;  $\hat{M}_i$  = total marked population;  $\hat{N}_i$  = total population estimate; SE = approximate standard error of the population estimate;  $\hat{\phi}_i$  = daily survival rate;  $\hat{\gamma}_i$  = daily loss rate.

Date (i)	Bailey					Manly-Parr					Jolly				
	$\hat{\alpha}_i$	$\hat{M}_i$	$\hat{N}_i$	1.96SE	$\hat{\gamma}_i$	$\hat{N}_i$	1.96SE	$\hat{\phi}_i$	$\hat{N}_i$	1.96SE	$\hat{\phi}_i$	$\hat{N}_i$	1.96SE	$\hat{\phi}_i$	
June 18	0.42	29.0	41.6	60.5	-0.47	42.0	31.8	0.86	69.0	62.7	0.69	69.0	62.7	0.69	
19	0.28	25.0	14.3	27.9	1.16	63.0	38.9	0.76	89.3	74.7	0.65	89.3	74.7	0.65	
21	0.37	24.5	42.9	52.3	0.18	64.6	37.8	0.94	66.2	39.5	0.82	66.2	39.5	0.82	
23	0.58	31.5	37.5	46.6	-0.03	48.6	21.3	1.17	54.3	22.5	0.97	54.3	22.5	0.97	
24	0.65	38.2	54.0	72.7	-1.04	46.8	23.5	1.01	58.8	27.4	0.69	58.8	27.4	0.69	
25	0.64	30.6	45.0	52.9	-0.35	48.0	33.0	0.91	47.9	19.8	0.80	47.9	19.8	0.80	
26	0.63	28.6	46.5	49.5	-0.19	43.5	10.5	1.85	45.2	10.0	1.37	45.2	10.0	1.37	
27	0.82	51.4	23.1	26.3	-0.04	63.8	43.1	1.18	62.7	25.0	0.77	62.7	25.0	0.77	
28	0.68	41.7	12.3	18.6	1.22	63.6	29.6	1.82	61.3	10.7	1.62	61.3	10.7	1.62	
29	0.94	79.0	5.0	9.9	1.70	80.0	70.1	0.74	84.0	65.1	0.59	84.0	65.1	0.59	
30	0.36	47.0	30.0	48.5	0.69	84.0	89.8	0.87	130.5	128.1	0.47	130.5	128.1	0.47	
July 2	0.43	26.4	34.2	67.0	0.82	69.0	32.6	0.65	61.4	29.9	0.86	61.4	29.9	0.86	
3	0.79	34.0	75.0	99.9	-0.91	40.4	14.0	0.53	43.0	17.8	0.64	43.0	17.8	0.64	
4	0.78	24.3	31.5	44.6	-0.12	25.7	4.3	—	31.2	13.6	—	31.2	13.6	—	

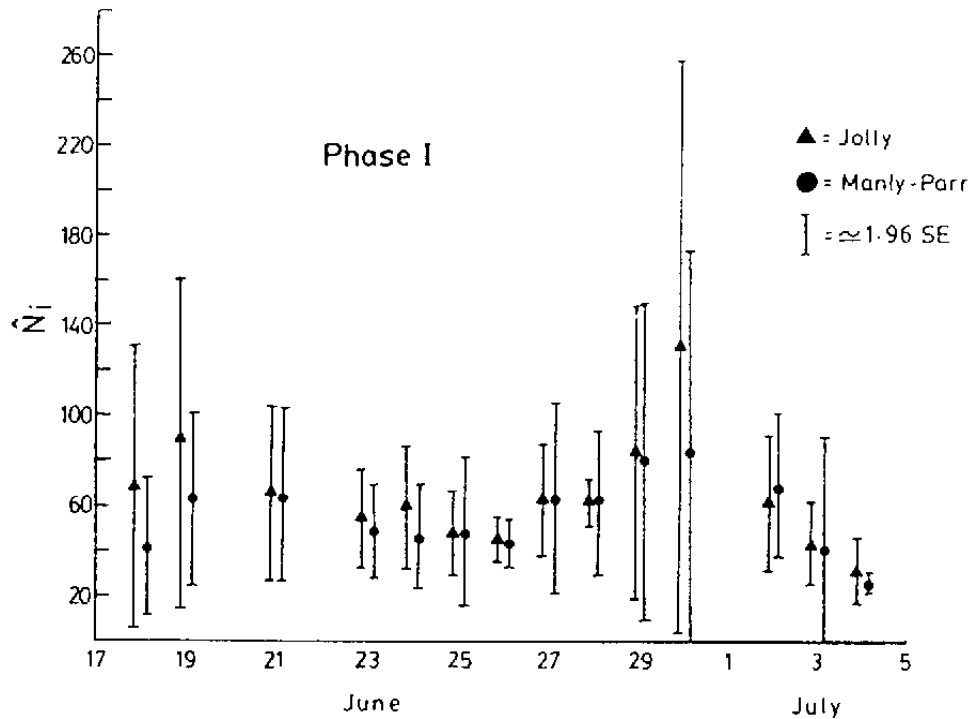


FIGURE 2. Population ( $\bar{N}$ ) estimates of *L. portoricensis* during Phase I study.

$\text{Ca}^{++}$ , and  $\text{Mg}^{++}$ . These nutrients are released in frass and could be important regulatory agents in succession. By decreasing the net production of early successional shrubs via consumption and increasing the availability of nutrients to later successional trees via defecation, *L. portoricensis* may assume an ecological importance in the forest greater than that predicted by its restricted distribution and overall abundance. This is critical, because early successional plants effectively and quickly immobilize nutrients in light-gap situations in tropical forests (Tukey, 1970).

The demographic attributes of *L. portoricensis* seem particularly adaptive to its existence in small isolated ephemeral habitats that are randomly dispersed spatially. Individual stick insects are usually philopatric and move less than 0.5 meters per day; this is to be expected for a nonvolant phytophagous insect. Almost all individuals were captured on the verdant vegetation that composed the diet of this species. However, some specimens (larger individuals) could disperse up to three meters per day, and low recapture rates also may indicate migration out of the study area. The low velocities for this species suggest an interesting dispersal-reproductive strategy, which is consistent with our observations of the ecology of *L. portoricensis*. The majority of recaptures on the grid were nymphs, and we suggest that these forms generally remain within a short distance of the location of hatching. On the other hand, many

TABLE 4. Population parameters estimated for multiple recapture data for *L. portoricensis* during Phase II. Symbols as in Table 3.

Date (i)	$\hat{\alpha}_i$	$\hat{M}_i$	Bailey			Manly-Parr			Jolly			
			$\hat{N}_i$	1.96SE	$\hat{\gamma}_i$	$\hat{N}_i$	1.96SE	$\hat{\phi}_i$	$\hat{N}_i$	1.96SE	$\hat{\phi}_i$	
July												
17	0.10	16.3	47.2	86.7	1.20	140.0	139.1	1.48	163.0	210.5	0.87	
18	0.43	29.7	55.6	64.9	-0.42	55.9	21.0	1.40	69.0	134.6	1.01	
19	0.48	43.3	18.9	29.7	0.06	58.3	19.9	0.53	90.2	40.5	0.71	
20	0.44	40.0	120.0	159.6	-1.28	86.4	68.8	0.48	90.9	59.6	0.75	
21	0.50	37.6	155.3	187.0	-0.40	67.6	25.8	1.24	75.2	29.6	0.68	
22	0.85	34.6	69.3	130.5	-0.52	41.3	13.4	0.94	40.7	7.7	1.20	
23	0.86	45.1	75.3	88.9	-0.99	44.0	13.0	1.40	52.4	12.5	0.49	
24	0.80	23.8	20.7	20.8	-0.45	38.8	19.4	2.22	29.8	5.8	1.96	
25	0.85	52.6	67.5	83.9	-1.10	46.4	10.5	1.35	61.9	15.7	0.37	
26	0.62	21.0	22.0	22.5	0.46	56.3	49.0	3.62	33.9	15.6	1.09	
28	0.80	38.3	46.0	63.4	-0.13	41.1	8.1	1.09	47.9	13.0	0.66	
30	0.76	28.6	25.2	28.9	0.15	35.7	12.9	1.00	37.6	11.7	1.14	
31	0.63	37.3	48.9	55.8	-0.55	45.1	18.1	0.75	59.2	24.8	.84	
August												
1	0.85	29.7	19.1	19.8	0.45	32.0	6.7	--	34.9	10.4	--	

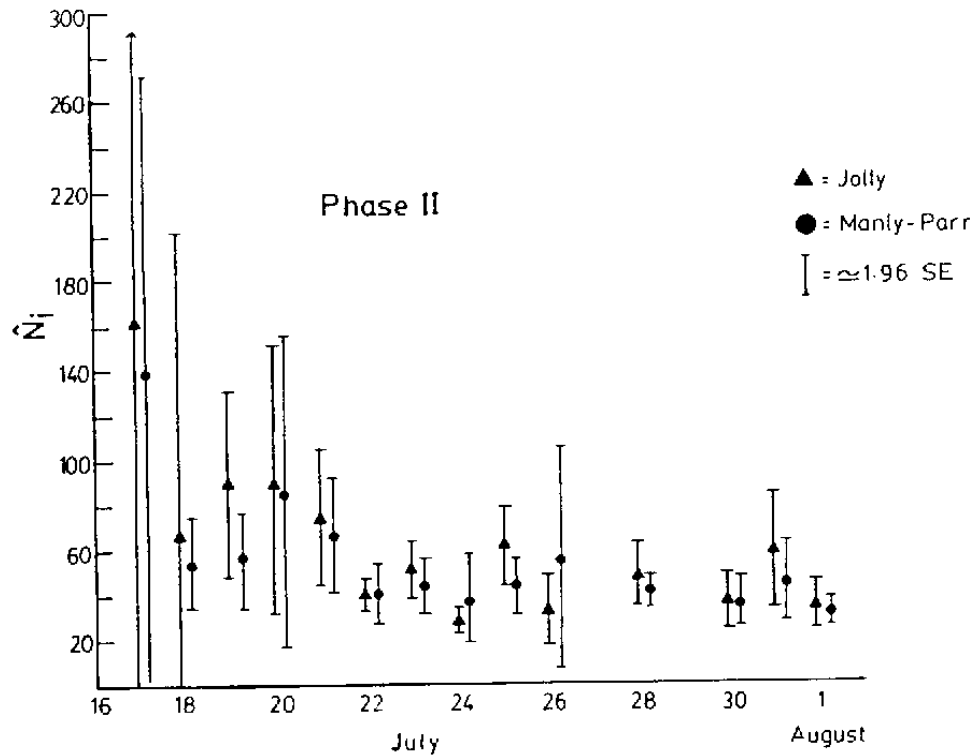


FIGURE 3. Population ( $\bar{N}$ ) estimates of *L. portoricensis* during Phase II study.

adults that were marked were never recaptured (Table I), and we believe that dispersal to new light gaps primarily occurs during this stage. The abundances of preferred foods for *L. portoricensis* are ephemeral in light-gap situations. The probability of resource depletion in such areas would be relatively high for this long-lived insect. It would therefore be advantageous for dispersal to occur in the adult stage when mobility is greatest, before resource abundance becomes low. This effectively minimizes competitive interactions among related individuals and reduces the probability of inbreeding within local populations as well.

Population trends of *L. portoricensis* are similar in Phases I and II despite the significant difference in the size (= age) structure of the population. The data suggest the addition of a cohort of individuals into the 10.1 to 20 mm size class at the beginning of Phase II and a corresponding increase of adults. The more mesic characteristics of Phase II apparently did not cause a significant increase in population density. The determination of survival rates for *L. portoricensis* remains enigmatic. Most phasmatids have the ability to live for long periods (Bedford, 1978), but given the high egg production of many species, it is probable that few specimens ever reach maturity. The survival rate for nymphs is difficult to assess because there was no way to permanently mark individuals that would persist from molt to molt. In addition, *L.*

*portoricensis* appears to breed year-round; hence, mixed age classes appear in the population at all times. Although stick insects derive protection from a complex of chemical, behavioral and morphological attributes, data on vertebrate foraging ecology in the Tabonuco forest suggest that *L. portoricensis* is preyed upon by frogs and lizards (Reagan et al., 1982; Garrison, personal observation). These predators may respond functionally to increased stick insect availability in light-gap zones, and we will be investigating these possibilities in future research. Parasitic infections by various species of biting flies have been reported for several neotropical phasmatids (Wirth, 1971); however, the realized detriment to the host has not been quantified. Thus, the low recapture rates evidenced by our data could reflect high mortality, which would considerably reduce the average life span of *L. portoricensis* in comparison with projections for other stick insects.

Clearly, many questions concerning the demography of *L. portoricensis* remain unanswered. Future research should concentrate on the stability of light-gap faunas in time as well as the magnitude of insect dispersal between such habitats. Perturbation studies documenting the relation between insect density and the presence of specific forage species would significantly contribute to understanding the dynamic aspects of phase-gap succession in forest ecosystems.

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