

Ontogenetic Changes in Resource Use by
the Puerto Rican Frog Eleutherodactylus coqui

A thesis presented to the Faculty
of the State University of New York
at Albany
in partial fulfillment of the requirements
for the degree of
Master of Science
School of Math and Science
Department of Biological Sciences

Karyn V. Townsend

1985

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ABSTRACT

Ontogenetic shifts in resource use are known to occur in many organisms including frogs with complex life cycles. These shifts have not been documented in any direct-developing anuran. Eleutherodactylus coqui is an endemic Puerto Rican frog having direct development. This species was examined for changes in its use of resources as it increased in body size (SVL) from hatching to adulthood. The resources examined were activity time, microhabitat, and food. Although changes in activity time did not occur among sizes of E. coqui, changes in the use of microhabitat and food did occur. Frogs were found on higher nocturnal perches and ate larger prey items as they increased in body size. Four factors were investigated as potentially contributing to changes in microhabitat use. They were moisture conditions, temperature, intraspecific competition and size-specific predation by the crab spider Stasina portoricensis. Moisture conditions affected all size classes while temperature affected only subadults. Neither intraspecific competition nor predation had any effect on the nocturnal perch height of any size class. Food size differed among size classes. Neither temperature nor moisture conditions had any effect on food size differences. Instead, an increase in gape size with increasing SVL appears to be responsible for the differences in prey size among size classes. The potential effects of ontogenetic shifts in resource use on amphibian communities are discussed.

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INTRODUCTION

Ecologists have long been interested in how animals use the resources available to them. The distribution of resources can determine the geographical and local distribution of a population (Heatwole, 1961, 1962; Jaeger, 1980). In a community, the way resources are partitioned among species can help us understand how a community is organized (Crump, 1971; Inger, 1969; Schoener, 1968; Toft, 1985; Toft and Duellman, 1979).

Toft (1985) reviewed the literature on amphibians and reptiles in an effort to understand the factors most responsible for resource partitioning. She found that both abiotic (moisture and temperature) and biotic (competition and predation) factors were important. Plethodon salamanders partition both habitat and food resources (Fraser, 1976a, b; Jaeger, 1970, 1971a, b, 1972; Lynch, 1985) and Toft argued that resource use was the result of an interaction between the salamanders' physiological tolerances and their response to competition for food and space. Toft (1980a, b, 1981) found that tropical litter anurans partition habitat, food (type and size) and time (diel and seasonal). In these communities, competition and the interactions between a frog, its prey and its predators were all factors responsible for the partitioning of resources. Most importantly, in both amphibian groups, a combination of abiotic and biotic factors determined resource use rather than any single factor.

While there are many studies of resource use among salamanders (e.g., Hairston, 1949, 1951), larval anurans (e.g., Heyer, 1973, 1974, 1976) and adult anurans (e.g., Jones, 1982; Pough, Stewart and Thomas,

1977; Stewart and Sandison, 1972; Toft, 1980a, 1981), few have examined ontogenetic differences in resource use within an anuran species (Alford and Crump, 1982; Jameson et al., 1973; Loman, 1979). Werner and Gilliam (1984) document ontogenetic shifts in resource use for communities with size-structured populations. Although size structured populations can be found in all taxa, examples are most abundant for ectotherms, especially invertebrates and fishes. In many size-structured populations body size increases by several orders of magnitude from birth or hatching to an organism's maximum size. Increases in body size can affect an organism's use of resources and its susceptibility to physical factors and predation. The resources most often affected are food, habitat, and activity time. Changes in the use of food as a resource may be the result of increases in the size of trophic structures (Christian, 1982; Fraser, 1976a; Toft, 1980a), intraspecific competition (Steinwascher, 1978, 1979) or changes in microhabitat (Simon and Middendorf, 1976). Habitat shifts may result from changing food habits, changing morphological and physiological tolerances (Jameson et al., 1973; Schoener and Schoener, 1970; Schoener, 1970), or avoidance of a size-specific predator (Crump, 1984; Wassersug and Sperry, 1977; Arnold and Wassersug, 1978). Activity time as a resource can also differ with changing body size (Simon and Middendorf, 1976). Changes in resource use with age in most anurans is obvious; tadpoles are aquatic herbivores while adults are semi-aquatic to terrestrial carnivores. Although ontogenetic changes in resource use in direct-developing frogs may be less dramatic, there are several reasons why it is still likely to occur. These frogs are ectotherms, they exhibit a wide range of body sizes and their

potential invertebrate prey occur in a wide variety of sizes.

The purpose of my study was to investigate ontogenetic changes in resource use in the Puerto Rican frog, Eleutherodactylus coqui, a direct-developing species. The use of three resources was examined; food, habitat, and activity time. Factors that were potentially responsible for ontogenetic shifts in resource use were investigated. These factors included temperature, moisture (both important to an ectotherm with permeable skin and a non-shelled egg), intraspecific competition and size-specific predation.

METHODS

Study Site

The study was carried out in the vicinity of the El Verde Field Station of the Center for Energy and Environment Research in the Luquillo Mountains of northeastern Puerto Rico (Caribbean National Forest, Luquillo Experimental Division). The study site is at 350 m in a second growth wet subtropical forest (Ewel and Whitmore, 1973). The climate there is weakly seasonal (Briscoe, 1966). The forest is dominated by tabanuco (Dacryodes excelsa) and contains secondary species including the sierra palm (Prestoea montana) and cecropia (Cecropia peltata). The understory contains many plants used by the frogs, especially Inga vera, Ruellia coccinea, Piper treleaseanum, Panicum adspersum, Guarea ramiflora, Prestoea montana, and Pilea sp.

Study Species

Eleutherodactylus coqui Thomas is a common frog found throughout Puerto Rico (Rivero, 1978). It occurs in high densities in the mid-elevation (350 m) forest around El Verde (Stewart and Pough, 1983). Frogs are nocturnal and spend the day in retreat and nest sites in the leaf litter, rolled palm fronds, or Cecropia leaves. At dusk, the frogs emerge and can be found moving from the ground to surfaces of leaves, rocks, tree trunks and branches. It is from these nocturnal perches that frogs forage and call (Drewry, 1970; Pough et al., 1983; Stewart and Pough, 1983; Woolbright, 1985). Although most activity occurs within 3 m of the ground, some individuals, especially females, climb to the canopy to forage (Stewart, 1985).

The eggs of E. coqui are laid in curled leaves or palm fronds where they undergo direct development and hatch as tiny frogs, 6-7 mm in snout-vent length (SVL). Hatchlings are known to leave nest sites within 6 days of hatching and take up residence in the leaf litter (Townsend et al., 1984; Townsend and Stewart, 1985). Hence, at any given time, frogs from 6.0 mm to the largest adults (maximum of 55.0 mm at El Verde) can be found coexisting in the forest.

For the purposes of this study, I defined three discrete size classes of frogs: juveniles, subadults and adults. Because vocal slits first appear in males at 24.5 mm SVL (M.M. Stewart, pers. comm.), adults were designated as frogs greater than 24.0 mm. Pre-adult frogs were further divided into juveniles (6.0 - 10.0 mm SVL) and subadults (10.5 - 24.0 mm SVL). These pre-adult size classes were based upon evidence of distinct clustering of smaller frogs (juveniles) on low

vegetation, as can be seen in Figure 1. Individuals using the canopy were not included in this study.

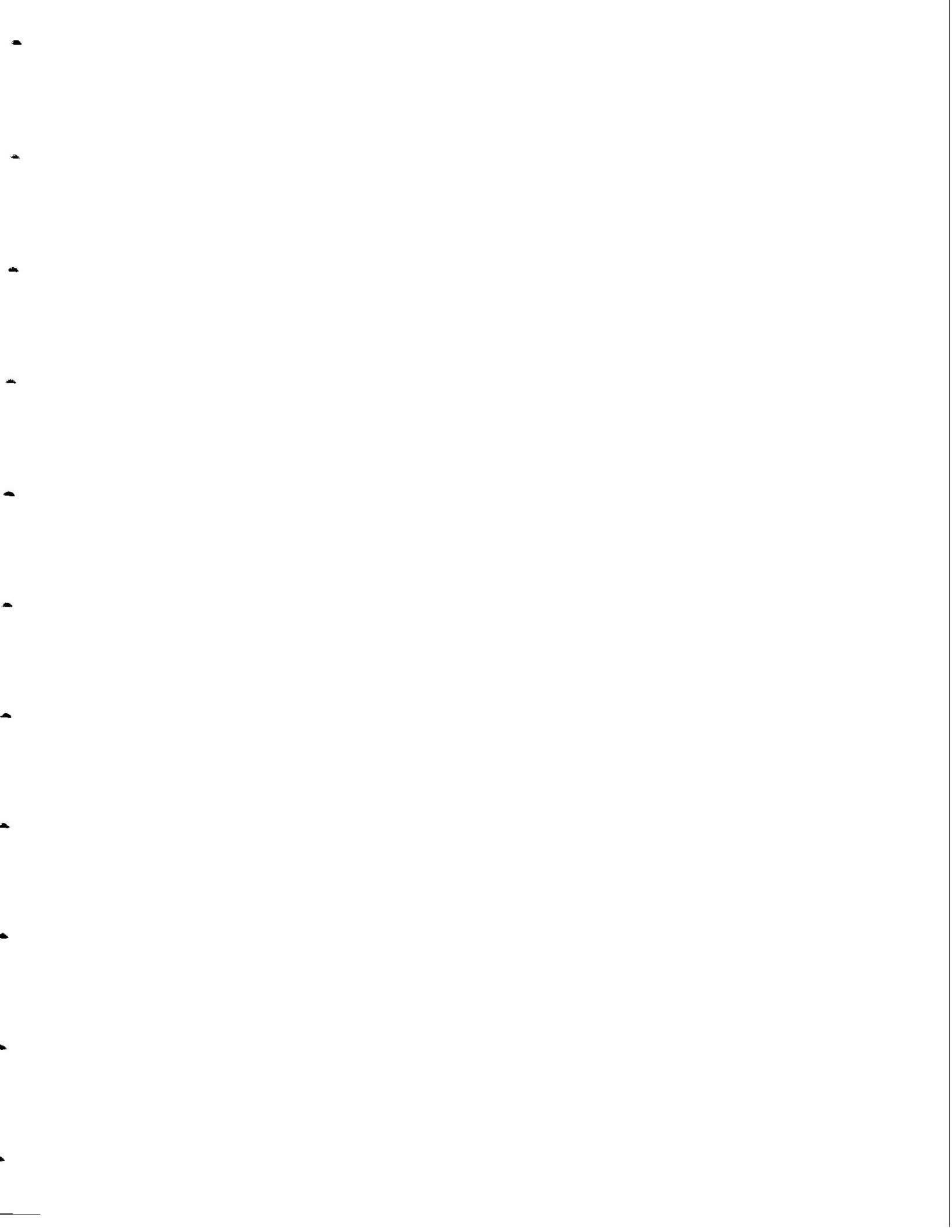
Monthly Surveys

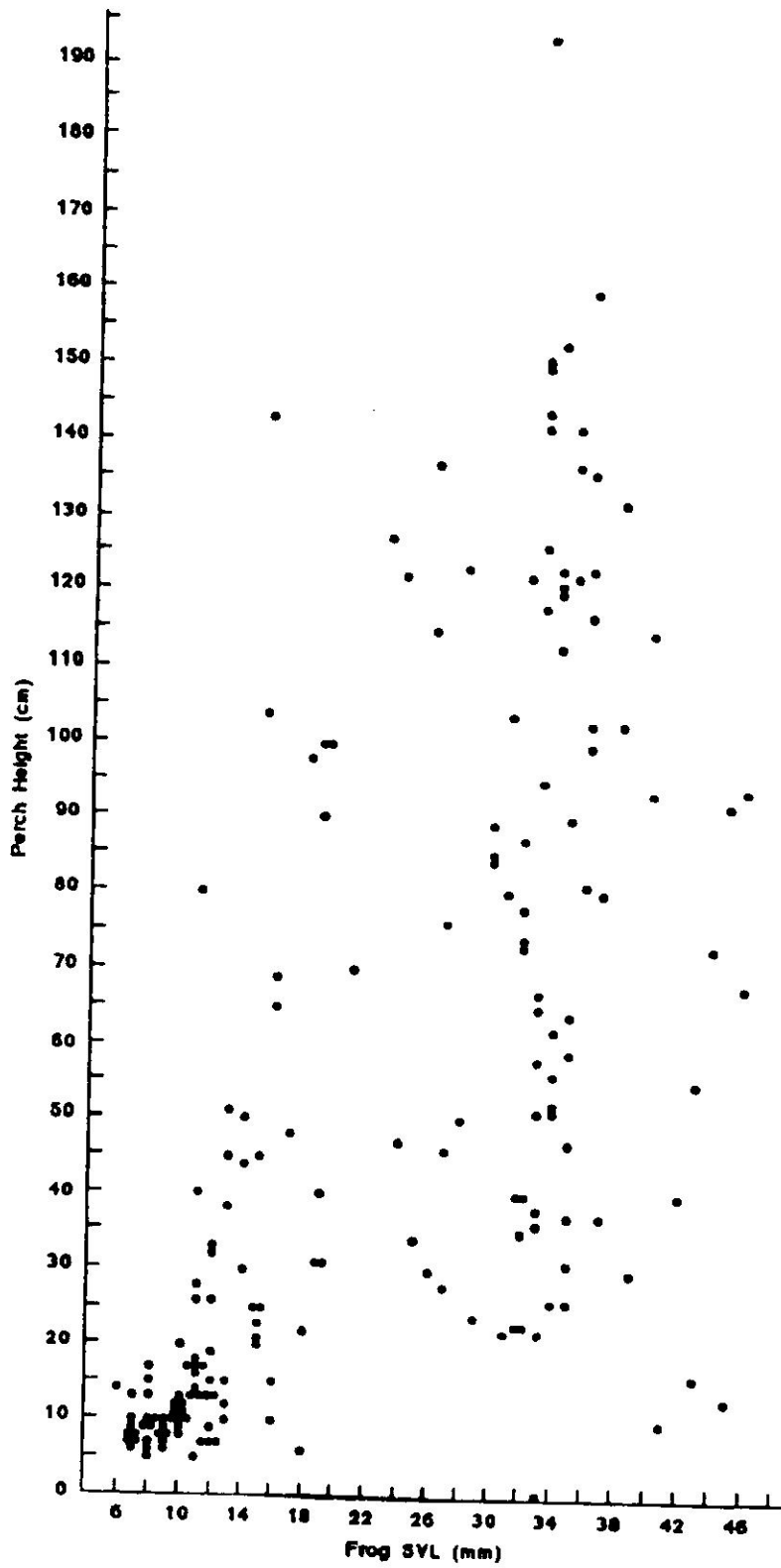
Field work was conducted during June through August of 1979 and January through July of 1980. Monthly nocturnal surveys of established areas in the forest were conducted to obtain the following data:

- 1) habitat use by the three size classes;
- 2) nocturnal perch height under a variety of temperature and moisture conditions; and
- 3) presence and perch heights of potential predators, especially crab spiders of the genus Stasina (Stasina = Olios of Formanowicz et al., 1981).

Surveys of nine pre-established plots in the forest were conducted monthly. Eight 5m X 5m plots were located in two areas of the forest. One group of four was located in a gently sloping hollow near the Sonadora River; the other four were in a ravine adjacent to the same river. The ninth plot was a 50m X 2m transect through the forest close to the El Verde Station. The 5m X 5m plots were surveyed on one night each month between 2000 and 2400 h. The transect was surveyed once a month for 1-4 consecutive nights. All surveys were done within a seven day period.

Using a headlamp, the ground and all substrates within 250 cm of the ground (rocks, roots, trunks, foliage, stems) were scanned for frogs. Frogs were captured, measured to the nearest 0.5 mm with a plastic mm ruler, and the height of their perch measured to the





nearest 0.5 cm. Frogs were released at their point of capture.

During these monthly surveys, crab spiders observed within the plots were also recorded. Body length of spiders was estimated by holding a plastic ruler parallel to them. The heights of their perches were also measured to the nearest 0.5 cm.

Food

To investigate the use of food by different size classes of coquies, I carried out two sets of observations during 1980. First, I took monthly samples of flying insects in the forest to determine prey availability. Second, I captured and killed frogs of different size classes and examined their stomach contents to determine foods eaten.

The availability of flying insects was measured at six heights in the forest: 0 cm, 25 cm, 50 cm, 100 cm, 150 cm and 200 cm above the ground. Translucent plastic drinking cups coated with Tack-trap (Animal Repellants, Inc.) were hung at the appropriate heights along a vertical string at seven locations in the forest. Strings were hung for three consecutive nights during each month from April through July, 1980. The strings were hung at dusk (1800-1900 h) and left in place all night. At dawn (ca. 0600 h) the cups from each string were gathered, wrapped individually in plastic wrap and refrigerated until analysis under a dissecting microscope. Analysis involved measuring and, when possible, identifying each insect to Order. Insect cup data were combined and grouped into a contingency table. Insects were grouped according to length on the basis of the range of prey sizes taken by each of the three frog classes.

On the second night of each monthly insect survey, between 2200 and 2400 h, 10 frogs in each of the three size classes were captured from perches in the forest. Height above ground was recorded for each frog. Each frog was placed immediately on ice and killed by hypothermia within an hour of capture. Frogs were later thawed and preserved in 10% formalin. After transfer to 40% propanol, stomach contents were removed and examined under a dissecting microscope. Insects were identified to order when possible, and length measured.

Temperature and Moisture

To measure the effects of temperature and moisture on the use of resources by size classes, temperature and relative humidity (measured with a sling psychrometer) were recorded one meter above the ground whenever a survey, experiment, or collection was made. Often relative humidity is used as the measure of available moisture. The activity of amphibians, with their permeable skin, is constrained by moisture conditions. For E. coqui, the availability of water for rehydration is likely to be more important than relative humidity (Van Berkum et al., 1982; Pough et al., 1983). Consequently, the moisture conditions of the litter and foliage were qualitatively assigned to one of five categories:

- 1) wet litter and wet foliage (standing water visible on both litter and leaf surfaces),
- 2) wet litter and dry foliage,
- 3) damp litter and dry foliage (litter is very moist but has no standing water),

- 4) dry litter and dry foliage,
- 5) raining.

Competition and Predation

Enclosure tents were used to confine specific combinations of frogs and crab spiders to small areas of the understory. If either large frogs or crab spiders are restricting the habitat used by small frogs, removal of the competitors (frogs) or predators (spiders) from enclosure tents could result in an expansion of the habitat used. Enclosures have been effectively used by other investigators to show release from competition (Connell, 1961; Grant, 1969) or predation (Menge, 1976). If competitive release were found, further studies would be needed to elucidate the type (exploitative or interference) and object (food, habitat) of competition. In my study, enclosure tents were used to determine whether removal of competitors or predators resulted in microhabitat expansion as measured by nocturnal perch heights of the frog size classes tested.

Five enclosure tents, each 158 cm tall by 120 cm square, were constructed with bamboo poles and covered with mosquito netting (mesh size of 0.5 - 2.0 mm). The ends of the bamboo poles were sunk into the ground and the perimeter of the frame was cleared of all vegetation, litter and small rocks. Small rocks held the netting firmly against the ground at the base of the tents. Tents were located in the forest adjacent to the main trail at El Verde. Criteria used in placement included an area of level ground, at least one Piper treleaseanum within the enclosure, an array of plants ranging in height from 5 to

160 cm, and easy access from the trail. To aid in estimating perch heights of frogs, strips of fluorescent flagging were tied at 10 cm height intervals on some of the taller plants in each tent. Tents were scanned with a headlamp.

The tents were erected during the day, followed by three nights during which any visible invertebrates or vertebrates, including frogs and crab spiders, were removed from the tent interiors. The schedule for introducing frogs and spiders (predators) in tents is shown in Table I. On the fourth night after set-up, experimental animals (10 juveniles, 4 subadults, 2 adults, or 2 spiders) were introduced. These densities are higher than those found in the forest understory. Experimental animals were collected from the surrounding forest and all introductions were made at 1900-2000 h. Only crab spiders with body lengths of 10 mm or more were used since, in a previous study (Formanowicz et al., 1981), smaller spiders were found not to attack frogs.

A series of five experiments was conducted, each consisting of some combination of one or more size classes of frogs or one size class and crab spiders. The first size class was introduced on the fourth night, and subsequent additions (if applicable) were made on the ninth and the fourteenth nights. As no scent-marking is known for E. coqui, the order of size class introductions was deemed unimportant as long as all possible size class combinations were tested. The five experiments were as follows:

- 1) juveniles alone; add subadults; add adults.
- 2) subadults alone; add adults;
- 3) adults alone; add juveniles;

Table I. Schedule for Animal Introduction to Enclosure Tents During 1980¹.

Days	Experiment Number				
	1	2	3	4	5
1-3	C	C	C	C	C
4-8	J	S	A	JCs	SCs
9-13	JS	SA	AJ		
14-18	JSA				

¹ C - Tents cleared, J - Juveniles present, S - Subadults present, A - Adults present, Cs - Crab spiders present.

4) juveniles and crab spiders;

5) subadults and crab spiders.

Each experiment was run once in each tent, following the schedule in Table II. There were five experimental runs, each begun on the same night. Surveys of the tents were conducted on every night of a run between 2100 and 2300 h, and were always conducted in the same order. During a survey, the height above ground and location within the tent of each frog and spider, and whether they were on a natural substrate or on the tent structure were recorded. Following each experiment, the tent netting was removed and at least five days passed before the next experimental run was started. This allowed for recolonization of the tent area by invertebrates, the frogs' food.

Statistics

All means are presented \pm one standard deviation. Differences among means were tested for significance by Student's t-test for paired comparisons, or by Kruskal-Wallis one-way ANOVA for groups. Frequency data were analyzed using the G-test. Alpha was set at 0.05 for all statistical tests.

RESULTS

Activity Time

All size classes of E. coqui are nocturnal. Frogs became active within one hour of dusk and returned to retreat sites by dawn. On this

Table II. Schedule for Operation of Enclosure Tents During 1980.

Date	Enclosure Tent Number				
	1	2	3	4	5
Feb 22	Exp 1	Exp 3	-	-	-
April 1	Exp 3	Exp 5	Exp 2	Exp 1	Exp 4
April 25	Exp 4	Exp 1	Exp 3	Exp 5	Exp 2
May 19	Exp 2	Exp 4	Exp 5	Exp 3	Exp 1
June 12	Exp 5	Exp 2	Exp 1	Exp 4	Exp 3
July 6	-	-	Exp 4	Exp 2	Exp 5

basis, there is no ontogenetic change in activity time by this species.

Microhabitat

In 1979, there was a positive correlation between frog size (SVL) and nocturnal perch height (Figure 1, $r = 0.616$, $p < 0.01$). To determine whether this relationship also held in 1980, perch height data from the monthly surveys were grouped according to the three size classes and mean heights of the groups compared. The mean perch height for juveniles was 13.7 cm (± 9.5 , $n = 198$, range = 3-100 cm), for subadults was 33.4 cm (± 35.5 , $n = 370$, range = 0-200 cm) and for adults was 74.3 cm (± 56.0 , $n = 70$, range = 0-235 cm). Differences were significant in all pairwise comparisons (Student's t-test, $p < 0.001$). Juveniles were found in densities of 1.2 frogs/100 m², subadults at 21.8 frogs/100 m², and adults at 4.1 frogs/100 m², in monthly surveys.

The effects of temperature and moisture on microhabitat use. In 1980, the highest recorded temperature at the station was 29.4 C and the lowest was 15.6 C. Temperatures at 2000 h varied less since that is neither the warmest nor the coolest time of day. During monthly surveys, the lowest temperature was 18.9 C on 20 March and the highest 23.9 C on 21 May (Table III). To increase sample sizes, the mean survey temperature for each month was computed. The coolest month was March with a mean temperature of 19.4 C; May was the warmest month with a mean temperature of 22.7 C. Mean perch height was not different

Table III. Weather Data for Nights of Insect and Frog Collections
in 1980.

Date	Max Temp (C)	Min Temp (C)	Moisture Conditions	
			litter	foliage
April 20	26.7	21.1	damp	dry
April 21	26.7	20.6	dry	dry
April 22	26.4	21.4	dry	dry
May 16	25.0	20.0	wet	wet
May 17	27.2	21.1	wet	wet
May 18	26.1	21.7	wet	wet
June 13	25.6	21.1	wet	
June 14	27.2	21.7	wet	
June 15	27.8	22.8	wet	
July 11	26.7	22.8	wet	wet
July 12	28.6	23.1	damp	dry
July 13	27.2	22.5	wet	wet

between these two months for adults or for juveniles. Subadults used perches that were significantly higher in May (48.5 ± 43.6 cm, $n = 51$) than in March (33.5 ± 37.8 cm, $n = 74$; $t = 2.05$, $p < 0.05$).

Because the above comparisons of frog perch height at different temperatures were made under a range of moisture conditions, the results may not reflect the effect of temperature alone (Beuchat et al., 1984). To eliminate moisture conditions as a confounding variable, I compared perch heights at various temperatures under the same moisture conditions.

Mean perch height when the temperature was below 21 C was compared with mean perch height when temperature was at or above 21 C, for each size class, using only those nights when both the litter and foliage were wet (Table IV). Only subadults showed a significant difference in mean perch height ($t = 3.29$, $p < 0.01$), perching higher when temperatures were at or above 21 C (48.5 ± 45.9 , $n = 37$) than when cooler (25.5 ± 33.6 , $n = 107$). The same comparisons were made using only nights when the litter was damp and the foliage dry (Table IV). Mean perch height was not different between these two temperature conditions for any of the three size classes.

For each size class, perch heights in the five moisture categories were compared using the Kruskal-Wallis one-way ANOVA. Adult heights were not significantly affected by moisture ($H = 7.89$, $p > 0.05$). Both juveniles ($H = 18.94$, $p < 0.001$) and subadults ($H = 10.15$, $p < 0.05$) were significantly affected by moisture conditions. To further understand the effect of moisture on juveniles and subadults, the mean perch height in each moisture category was compared to every other moisture category using the Student's t -test (Figure 2 and Table

Table IV. Perch Heights (in cm) of Frog Size Classes in Monthly Surveys.

Conditions		Juveniles	Subadults	Adults
Wet litter +	Mean	11.5	25.5	71.9
wet foliage;	SD	3.8	33.6	53.1
below 21 C	n	13	107	7
Wet litter +	Mean	13.3	48.5	113.1
wet foliage;	SD	5.2	45.9	61.6
above 21 C	n	48	37	11
Damp litter +	Mean	26.7	26.7	50.9
dry foliage;	SD	36.1	22.5	54.5
at 21 C	n	6	66	15
Damp litter +	Mean	12.9	39.1	48.7
dry foliage;	SD	4.7	19.4	22.1
21 - 26.7 C	n	9	10	3



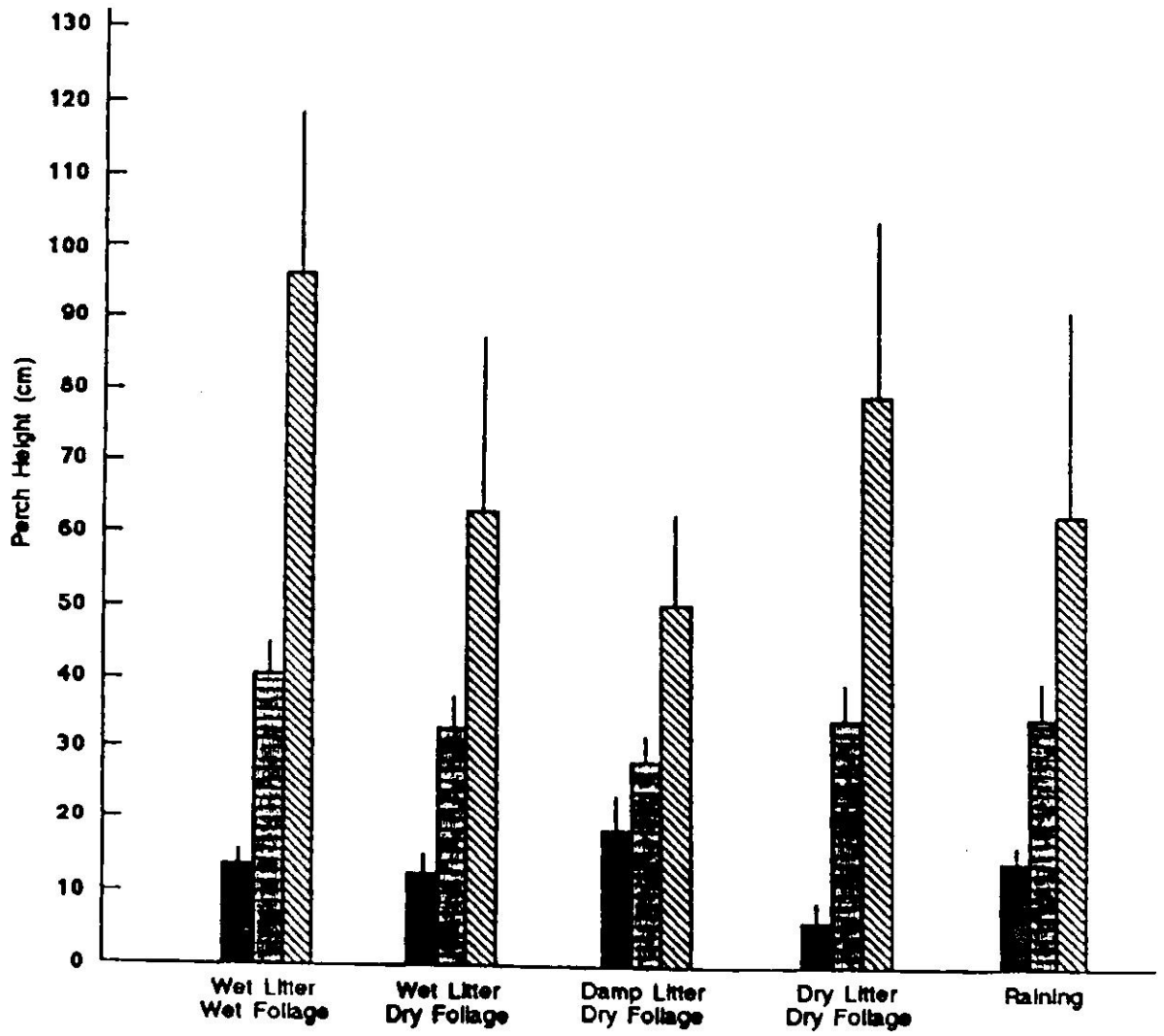


Table V. Comparisons of Mean Frog Height in Monthly Surveys under Different Moisture Conditions.

litter/foilage vs. litter/foilage		Juveniles		Subadults	
		t	df	t	df
wet/wet	wet/dry	1.000	104	1.169	155
wet/wet	damp/dry	1.652	106	2.191	170
wet/wet	dry/dry	4.050	89	0.902	149
wet/wet	raining	0.571	140	0.937	138
wet/dry	damp/dry	1.108	36	0.900	135
wet/dry	dry/dry	3.980	29	0.246	114
wet/dry	raining	0.902	80	0.046	103
damp/dry	dry/dry	1.476	21	1.341	129
damp/dry	raining	10.959	72	0.800	118
dry/dry	raining	2.184	65	0.175	97

V). For juveniles, three comparisons were significantly different; (1) wet litter and dry foliage vs. dry litter and dry foliage ($t = 3.88$, $df = 29$, $p < 0.01$), (2) wet litter and wet foliage vs. dry litter and dry foliage ($t = 4.05$, $df = 89$, $p < 0.001$), and (3) raining vs. dry litter and dry foliage ($t = 2.18$, $df = 65$, $p < 0.05$). Only one subadult comparison was significant, wet litter and wet foliage vs. damp litter and dry foliage ($t = 2.19$, $df = 170$, $p < 0.05$).

Moisture conditions in the forest also were recorded during the tent enclosure experiments on every night of each run. The effect of moisture conditions on the activity of the frogs was assayed by calculating the percentage of frogs originally put into the tent that were visible on a given survey night (Table VI). Juveniles and subadults showed responses to moisture conditions that were similar to those found during monthly samples. The highest percentage of frogs was found when the litter was wet; the lowest percentage (except for adults) when the litter was dry. An intermediate percentage was active when it was raining. Raindrops were seen dislodging juveniles from their perches in the forest; this may explain why fewer frogs are seen when it was raining than when the litter was wet. Adult behavior in the tents differed somewhat from adult activity in monthly surveys, with the lowest percentage of frogs visible under the wettest conditions (wet litter and wet foliage, raining).

In summary, I found no significant effect of temperature on perch height in juveniles or adults; subadults used perches that were significantly higher on warm wet nights. Moisture conditions affected perch heights of juveniles and subadults, but not adults. Juveniles were found significantly higher when the litter was wet or when it was

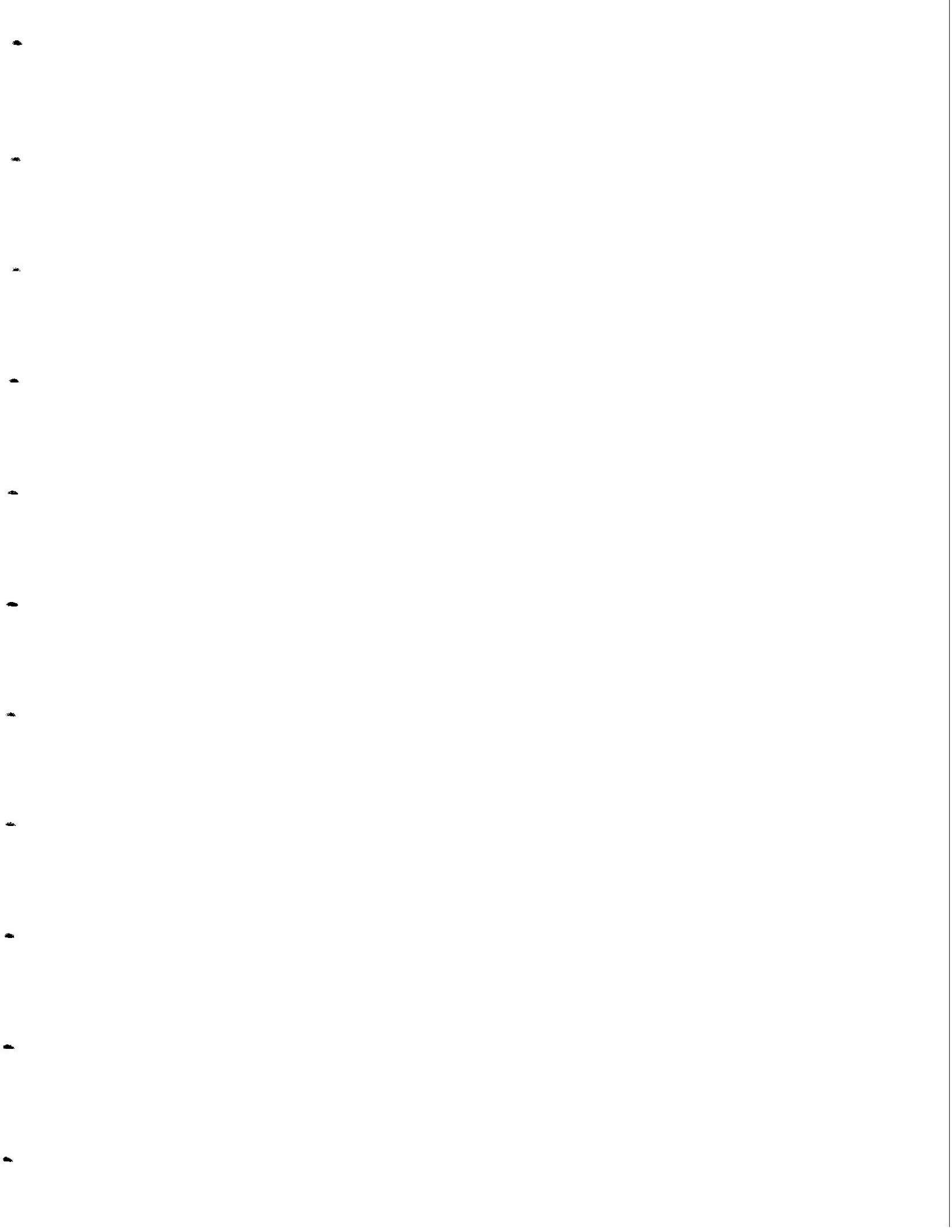
Table VI. Percentage of Frogs Active (between 2100-2300 h) in
Enclosure Tents Under Five Moisture Conditions in 1980.

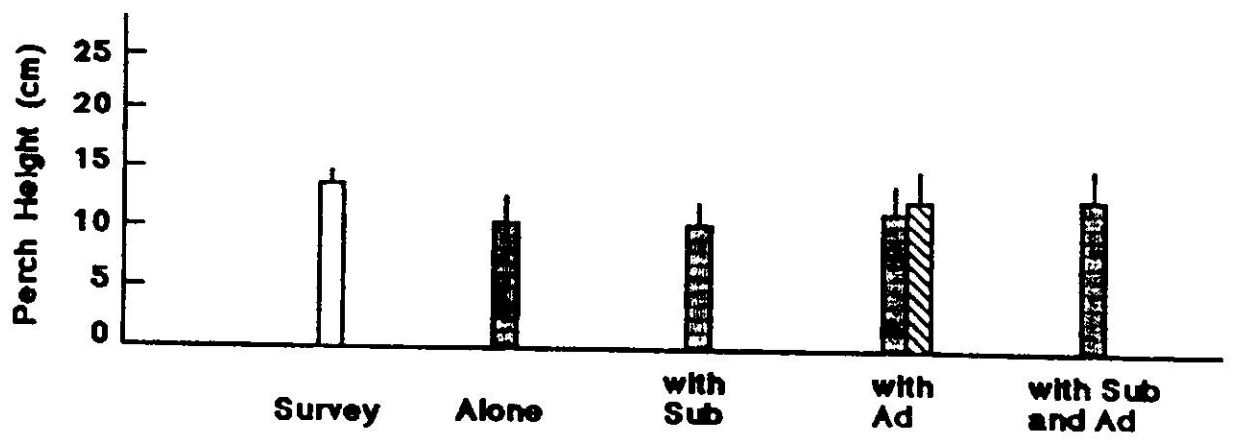
Moisture Conditions Litter/Foliage	Size Class		
	Juveniles	Subadults	Adults
Wet/Wet	19	81	47
Wet/Dry	18	88	66
Damp/Dry	7	68	62
Dry/Dry	2	44	60
Raining	7	79	58

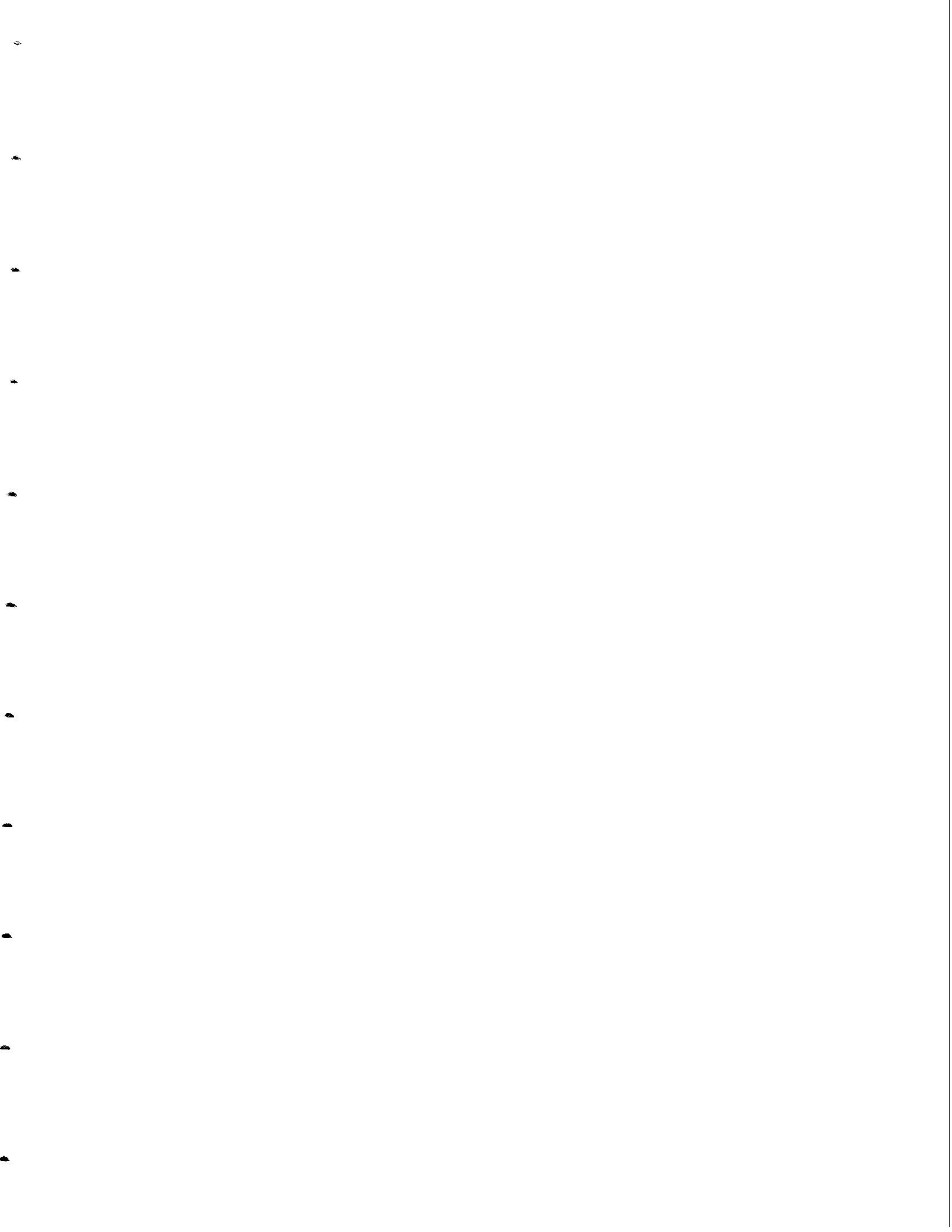
raining than when the litter was dry. Subadults were found highest when the litter and foliage were wet. Tent data corroborate the perch height data in that more juveniles and subadults were active on wet than on dry nights.

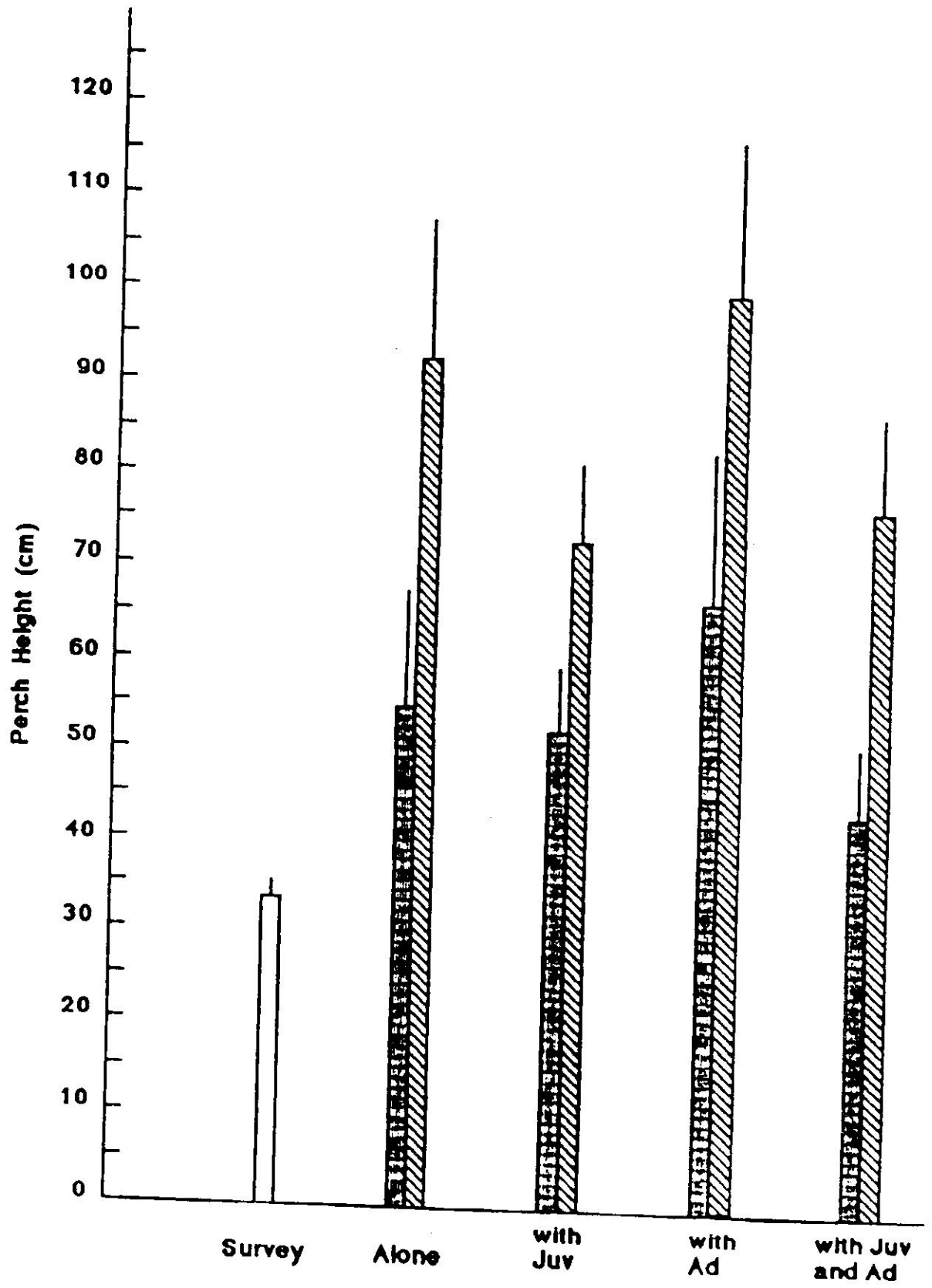
The effect of competition on microhabitat use. To determine whether intraspecific competition had any effect on frog perch height, the mean perch height of each size class when alone in the tent was compared with perch heights when in the presence of one or both other size classes. For example, for juveniles, I compared mean perch height for (1) juveniles alone (Experiment 1, days 4-8), (2) juveniles with subadults present (Experiment 1, days 9-13), (3) juveniles with adults present (Experiment 3, days 9-13) and (4) juveniles with both subadults and adults present (Experiment 1, days 14-18). The mean perch heights for each size class under the four conditions were compared using a Kruskal-Wallis one-way ANOVA. No significant differences were found in mean perch height for any of the three size classes.

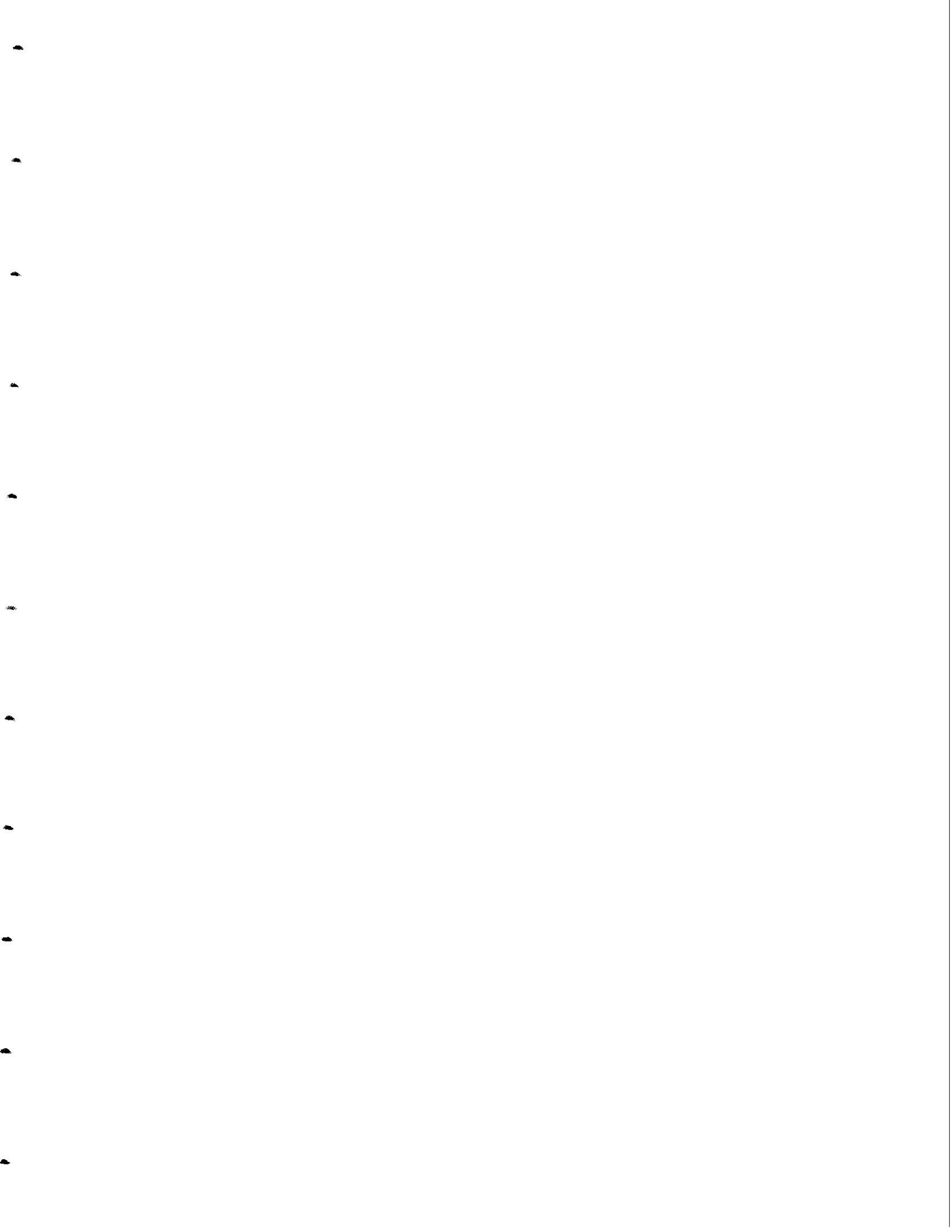
While in the tents, both subadults and adults used the tent structure (bamboo frame and netting) for perches, while juveniles did not. To see whether the tent structure had any effect on perch heights of adults and subadults, the mean perch heights of frogs in the survey plots were compared to their mean perch heights when in the tents with all size classes present (Figures 3-5). Although pairwise comparisons showed no difference in perch height for juveniles or adults, subadults used significantly higher perches when inside the tents ($t = 7.8764$, $p < 0.05$).

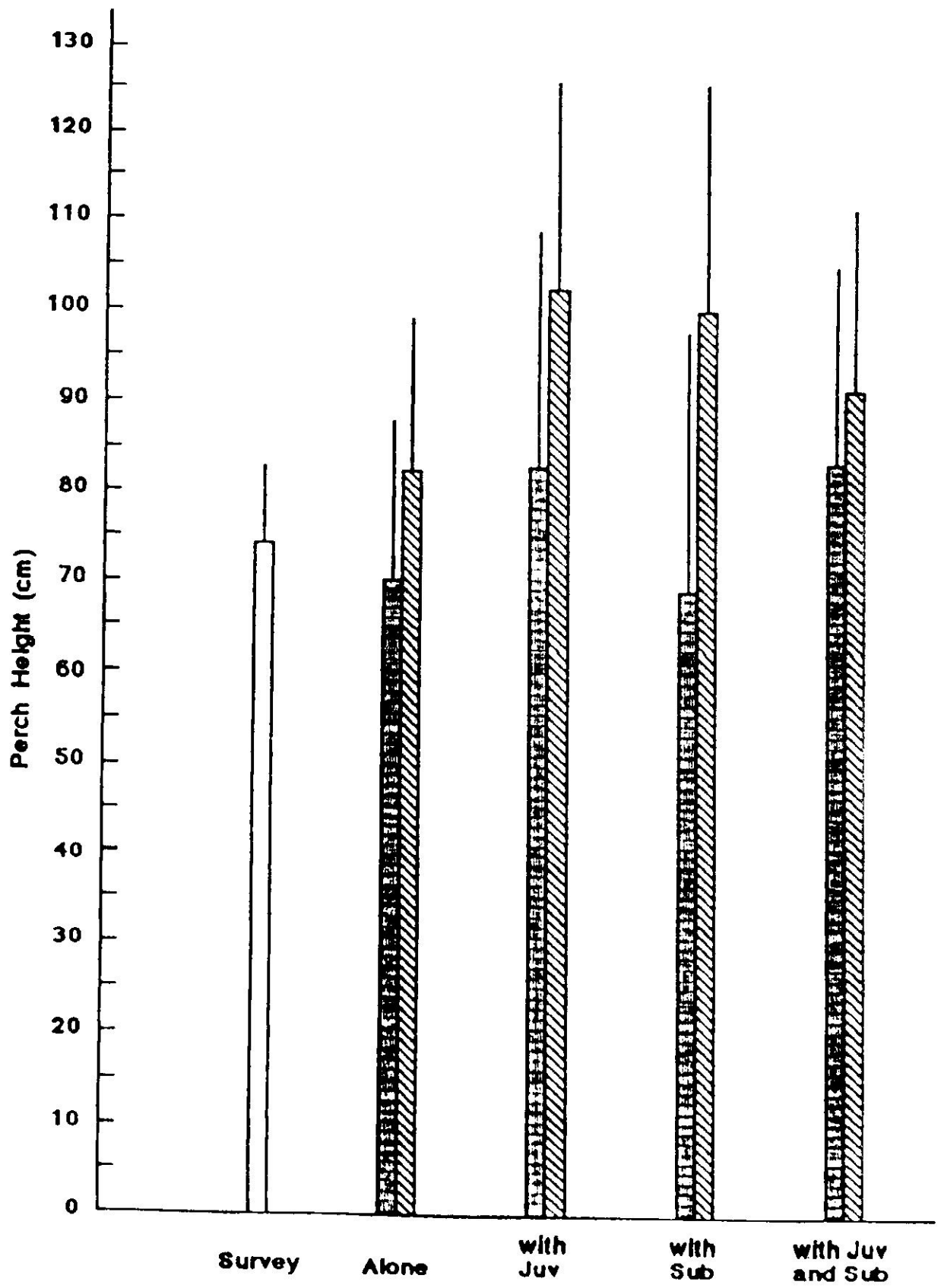












The effect of predation on microhabitat use. The mean perch height of 70 crab spiders, observed during monthly surveys, was 39.8 cm (\pm 38.2, range = 8-203 cm), significantly different from the mean perch height of juveniles (13.7 cm; $t = 8.90$, $p < 0.001$) and of adults (74.3 cm; $t = 4.259$; $p < 0.001$). Mean perch heights of crab spiders and subadults were not significantly different.

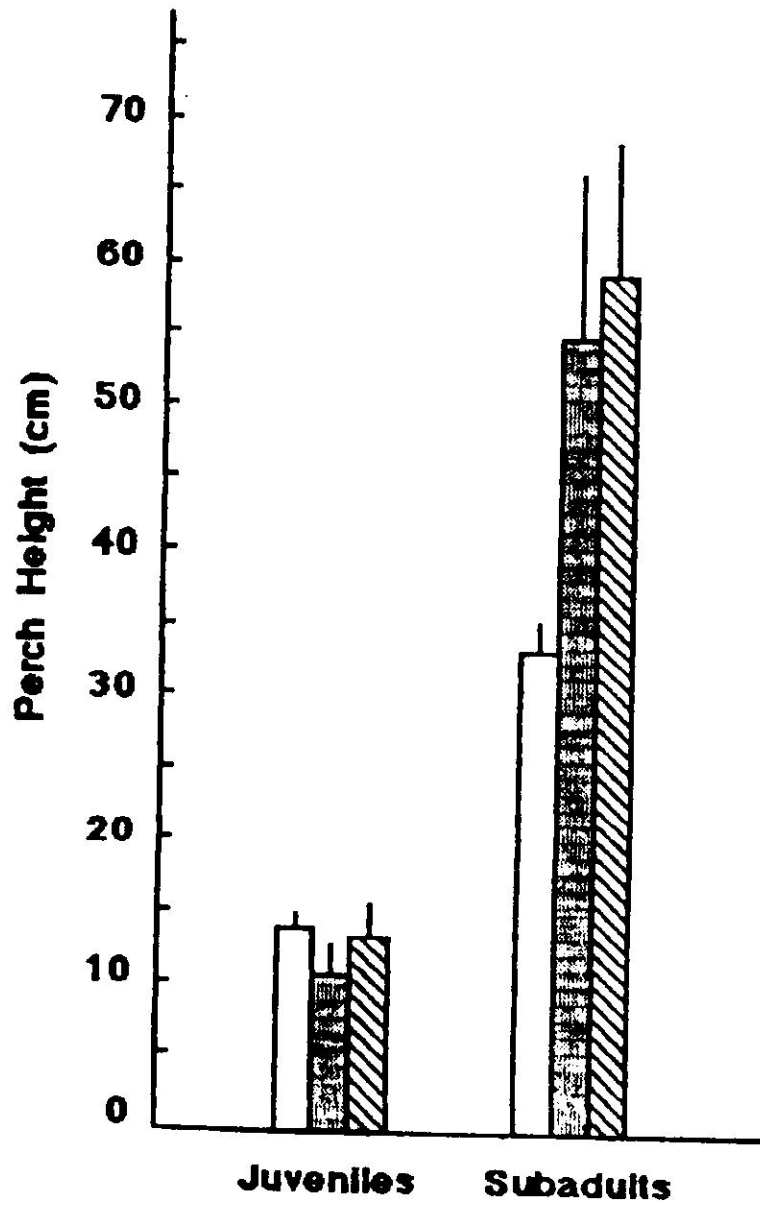
In the tent enclosure experiments, Experiments 4 and 5 were designed to measure the interaction of juveniles and subadults, respectively, with their potential predator, the crab spider Stasina portoricensis. The mean perch height of all crab spiders in the tents was 74.8 cm (\pm 36.7, range 25-130 cm, $n = 11$), significantly higher than in monthly surveys ($t = 2.84$, $p < 0.05$; Table VII). The mean perch heights of juveniles in Experiment 4 and of subadults in Experiment 5 did not differ from their respective perch heights in monthly plot surveys (Figure 6). In Experiment 4, mean perch height of juveniles differed significantly from that of spiders ($t = 6.82$, $p < 0.05$). Subadult and spider perch heights were not different in Experiment 5.

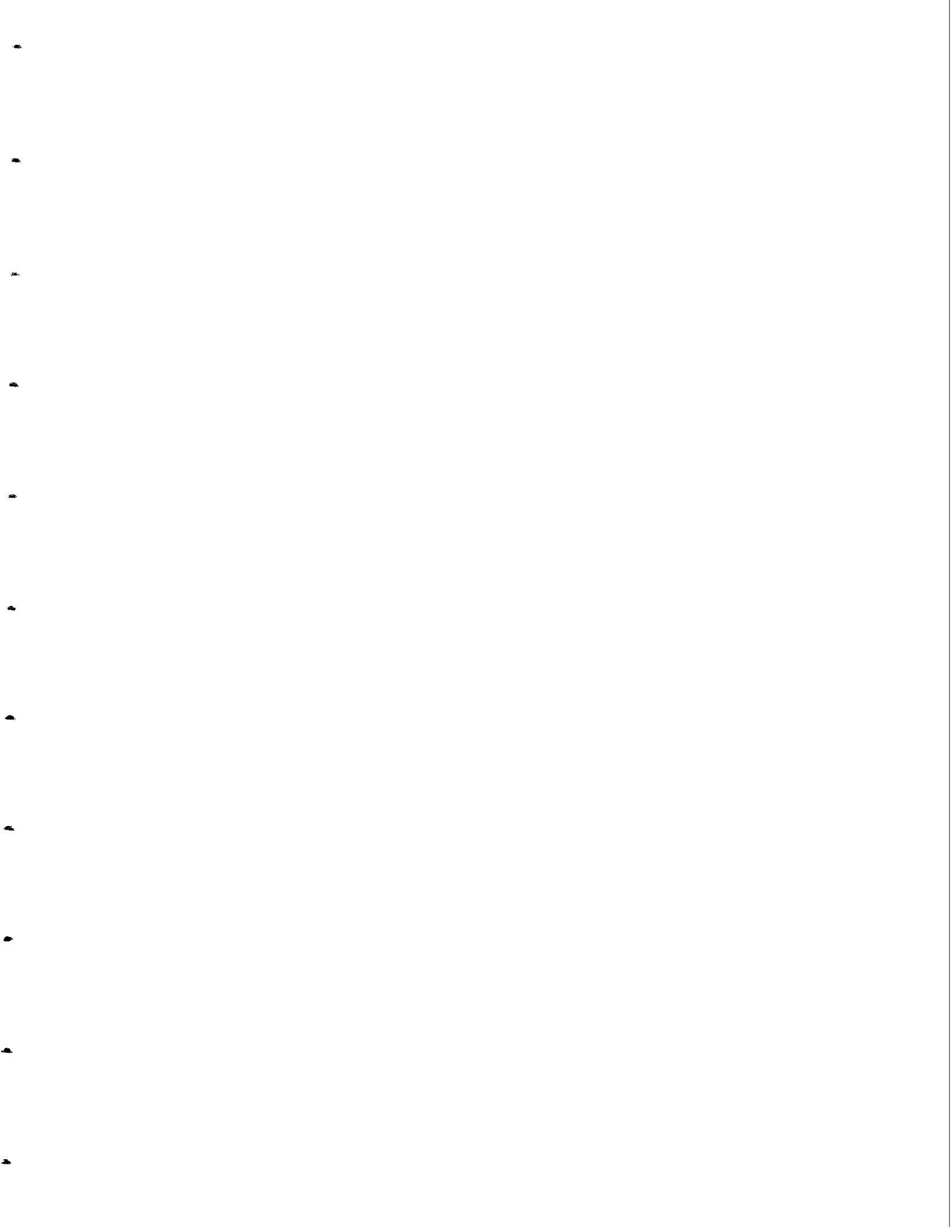
In Figure 7 the numbers of frogs located in the monthly surveys from January to June are presented in 1 mm increments of SVL. The numbers of frogs with SVLs of 7-14 mm are fairly constant. There is a dramatic decline in the number of frogs with SVLs of 14-17 mm and a second drop in frog numbers at 19-22 mm SVL. The largest frogs that Stasina can catch and eat are 17 mm SVL. When presented with 14-17 mm frogs, Stasina consumed them 58% of the time (Formanowicz et al., 1981). Perhaps crab spiders are perching where the largest frogs they

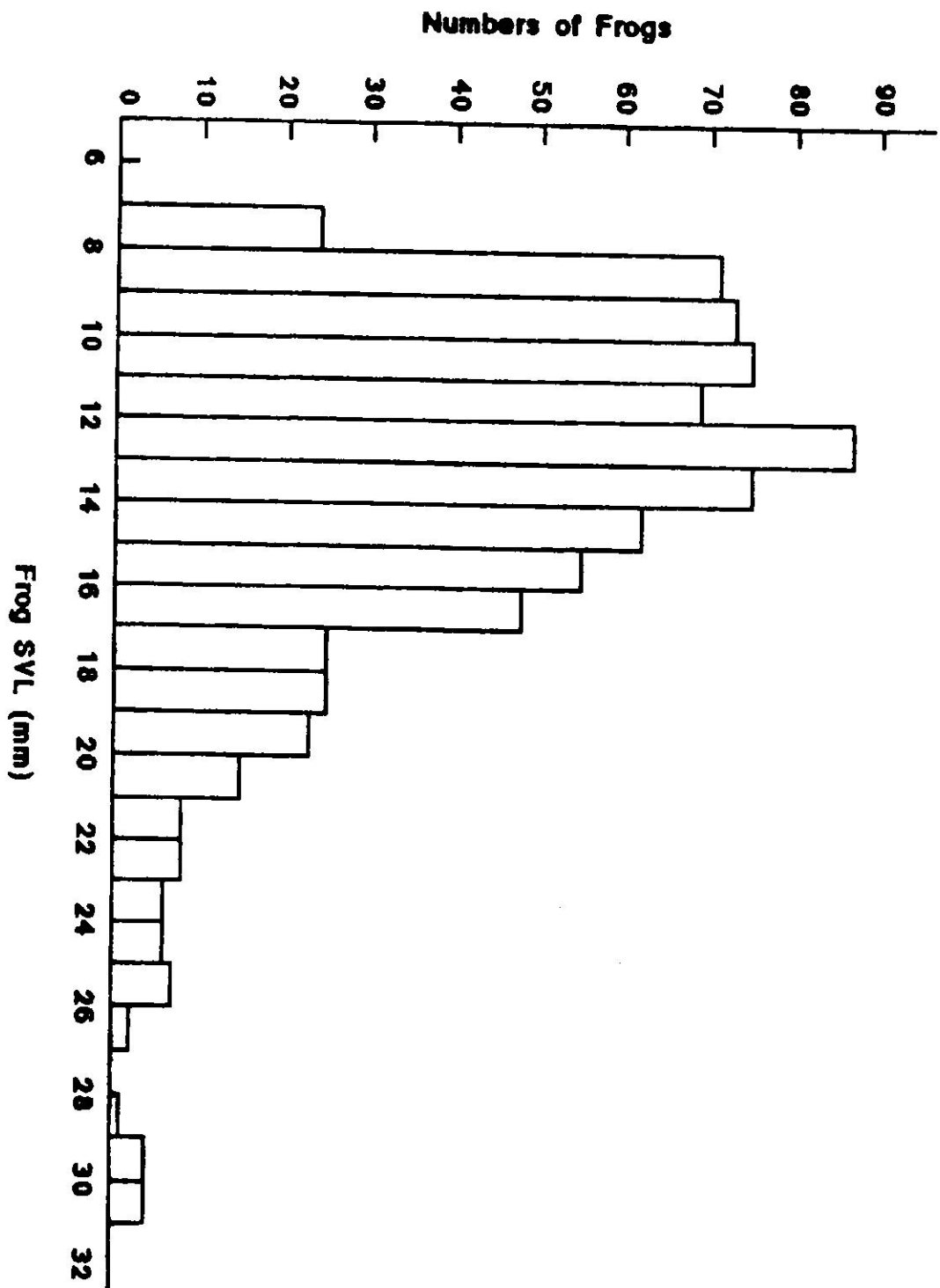
Table VII. Mean Perch Heights (in cm) of Spiders in Monthly Surveys and Tents.

	Monthly			Tents					
	Surveys			on contents			on contents and tents		
	Mean	SD	n	Mean	SD	n	Mean	SD	n
With juveniles				75.5	37.4	6	94.7	50.1	15
With subadults				74.0	40.1	5	118.3	43.6	24
With all size classes	39.8	38.2	70						









can eat are found. Predation by Stasina may be responsible, in part, for the decline in the numbers of frogs (14-17 mm) seen in Figure 7.

Food

Prey type. The stomach contents of 86 frogs were examined; 27 adults, 30 subadults, and 29 juveniles. The stomachs of adults contained an average of 2.5 prey items (\pm 2.9, range = 0-14), subadults an average of 7.7 prey items (\pm 5.0, range = 0-20), and juveniles an average of 4.3 prey items (\pm 2.8, range = 0-13). Ninety-one percent of the 517 prey items recovered from all frogs were identified to Order (Table VIII). The majority of these were ants; in adult stomachs 62% of all prey items were ants, in subadults 81.5% were ants, and in juveniles 72% were ants. Volumes of all prey were calculated by considering each prey item to be a cylinder, and taking prey width (diameter) to be a function of prey length. By volume, adult stomachs were found to contain 2.3% ants, subadults contained 55.8% ants and juveniles contained 62.3% ants. Of the 396 ants found in frog stomachs, only 12 were greater than 3.0 mm in length (Table IX). When considering the volume of prey items within the size range taken by juveniles, 0.5-3.0 mm, ants comprised 88.4% of adult stomach contents, 79.3% in subadults, and 62.3% in juveniles. Ants are abundant at El Verde (R. Garrison, pers. comm.). Most are small, but quite a few are larger than 3 mm in body length. Considering the above, differences in the volume of ants eaten by the three size classes do not reflect differences in preferences for ants.

Table VIII. Number of Prey Items in the Stomachs of 86 Eleutherodactylus coqui Collected April-July 1980, Organized by Taxonomic Category.

Prey Taxon	Size Class		
	Juveniles	Subadults	Adults
Crustacea	-	-	4
Diplopoda	-	1	-
Arachnida	3	3	3
Insecta			
Orthoptera	-	2	5
Hemiptera	1	2	-
Homoptera	1	1	-
Coleoptera	11	29	5
Lepidoptera	-	-	1
Diptera	-	-	1
Hymenoptera			
ants	98	257	41
non-ants	-	-	1
Unidentified			
larvae	6	5	3
adults	16	15	2

Table IX. Number of Prey Items in the Stomachs of 86 Eleutherodactylus coqui Collected April-July 1980, Organized by Prey Length (mm).

Prey Length	<u>Juveniles</u>			<u>Subadults</u>			<u>Adults</u>		
	ants	other	total	ants	other	total	ants	other	total
0.5	0	11	11	0	16	16	0	0	0
1.0	25	6	31	53	5	58	5	0	5
1.5	59	3	62	115	2	117	6	3	9
2.0	14	14	28	62	17	79	10	1	11
2.5	0	3	3	9	6	15	6	1	7
3.0	0	1	1	10	4	14	10	1	11
3.5				1	1	2	2	4	6
4.0				0	2	2	1	3	4
4.5				-	-	-	1	0	1
5.0				7	2	9	-	-	-
5.5				0	1	1	-	-	-
6.0				-	-	-	0	2	2
7.0				0	1	1	0	1	1
8.0				0	1	1	0	1	1
>8.0							0	8	8
Totals	98	38	136	257	58	315	41	25	66

Prey size. The range of prey length taken by each size class of frogs was different (Table IX); 1.0-22.0 mm for adults, 0.5-8.0 mm for subadults, and 0.5-3.0 mm for juveniles. Mean prey length was significantly different for all pairwise comparisons among frog size classes, with adults taking prey 4.1 ± 4.2 mm ($n = 66$) in length; subadults, 1.8 ± 1.0 mm ($n = 314$); and juveniles, 1.4 ± 0.5 mm ($n = 137$).

The effects of temperature and moisture on diet. The minimum and maximum temperatures were similar on nights that frogs were collected in April (26.7 C, 21.1 C), May (27.2 C, 20 C) and June (27.8 C, 21.5 C), while they were warmer during July (28.6 C, 22.5 C)(Table III). To test whether temperature had any effect on the length of prey found in stomachs, the mean length of prey in stomachs of frogs collected in May was compared to that from stomachs of frogs collected in July. No significant differences in mean prey length were found between the two months for any of the three size classes.

The April collection night was dry and no rain had fallen during the 48 hours prior to collecting (Table III). The collection nights during all other months were wet with rain having fallen during the previous two days. To see whether moisture had an effect on the size of prey eaten, mean prey length for the night in April was compared with that of May for each size class. Only subadults showed a significant difference. Subadults ate larger prey in May ($t = 2.24$, $df = 91$, $p = 0.024$). No significant differences in mean SVL between frogs collected in April and May were found for any size class.

In summary, the type of prey eaten by the frogs did not differ

among size classes although size of prey did. Prey length was positively correlated with frog SVL. Temperature did not affect the size of prey eaten by any size class. Moisture had a significant effect on prey length only for subadults, which took larger prey on wet nights.

The availability of flying insects. The data from the insect cups (Table X) were analyzed using a contingency table (Table XI). There was a significant change in the relative frequency of the three insect size classes as a function of cup height ($G = 84$, $df = 10$, $p < 0.005$). Smaller items are much more abundant at lower levels. Larger prey items (> 8 mm in body length) do not differ in abundance at the levels sampled (Table XI).

DISCUSSION

This paper examines the use of three resources: activity time, habitat, and food by three size classes of a Puerto Rican frog, Eleutherodactylus coqui. Time of activity did not differ among size classes; all were nocturnal. The use of habitat and food resources changed with increasing body size. In the following discussion, the use of microhabitat and food and the factors responsible for changes in the use of these two resources will be addressed.

Microhabitat as a Resource

Ontogenetic shifts in microhabitat use do occur in E. coqui. Mean

Table X. Numbers of Insects Trapped on Cups at Six Heights Above the Ground, Organized by Insect Length (mm).

Insect Length	Cup Height (cm)						Total
	0	25	50	100	150	200	
0.5	33	15	18	19	11	11	107
1.0	617	205	151	115	121	130	1342
1.5	118	72	44	51	50	53	388
2.0	218	130	123	89	91	104	755
2.5	72	64	59	60	60	65	380
3.0	122	99	97	63	84	71	536
3.5	20	13	12	11	5	7	68
4.0	55	35	72	25	32	19	238
4.5	10	15	15	5	2	5	53
5.0	34	26	34	14	9	6	123
5.5	3	2	3	0	2	2	12
6.0	15	19	11	3	10	7	65
6.5	4	2	0	1	0	0	7
7.0	5	11	3	3	1	7	30
7.5	1	0	2	1	0	0	4
8.0	4	9	1	1	2	1	18
>8.0	18	27	10	16	15	19	105
Totals	1349	744	656	480	495	507	4231

Table XI. Numbers of Insects Trapped by Cups at Six Heights Above the Ground, Organized by Intervals of Insect Length (mm) (Percentage of Row Totals in Parentheses).

Interval of Insect Length	Cup Height (cm)						Total
	0	25	50	100	150	200	
0.5-3.0	1180 (33.6)	585 (16.7)	492 (14.0)	400 (11.4)	417 (11.9)	434 (12.4)	3508
3.5-8.0	151 (24.4)	132 (21.4)	154 (24.9)	64 (10.4)	63 (10.2)	54 (8.7)	618
> 8.0	18 (17.1)	27 (25.7)	10 (9.5)	16 (15.2)	15 (14.3)	19 (18.1)	105
Totals	1349	744	656	480	495	507	4231

nocturnal perch heights of the three size classes are significantly different (juveniles 13.7 cm; subadults 33.4 cm, adults 74.3 cm). Four factors seemed likely to be responsible for this change in microhabitat use. Differences in body size are likely to result in different physiological tolerances to temperature and moisture. Large frogs could restrict nocturnal perch height of small frogs. Avoidance of size specific predation could also be responsible for differences in nocturnal perch heights.

Competition. The effect of competition on perch height was tested using various combinations of frogs in forest enclosure tents. The significantly higher perch heights of subadults in the enclosure tents (in the presence of all size classes) than in the monthly surveys indicates that frogs were in the tents long enough to assess and use the tent structure. Subadults used the tent structure as a perch while juveniles rarely did so. Presumably, frogs were also left in the tents long enough to show competitive release when all other size classes were removed if competition is an important factor in microhabitat use. No significant change between frog perch height when alone in the tents and when with another size class(es) was found for any size class. Field observations corroborate the experimental evidence. Aggressive encounters between frogs could be an indication of interference competition. Although aggressive interactions over retreat and nest sites have been seen (Townsend et al., 1984; Stewart, pers. comm.), few aggressive interactions for perches have been observed in the field. Exceptions are the aggressive calls and aggressive encounters seen in defense of call sites by males (Reyes

Campos, 1971; Narins and Capranica, 1978).

Rather than reacting aggressively when they meet in the forest, on many occasions two juvenile frogs use the same leaf as a nocturnal perch. Therefore both field and experimental observations indicate that competition for nocturnal perches is not currently responsible for microhabitat use.

Predation. The enclosure tents showed no significant difference in perch heights used by a size class when alone from those used when with the crab spider Stasina. Therefore avoidance of the predator Stasina does not seem to be an important factor in microhabitat use. Nor do coquies avoid trees with other predators (scorpions, tarantulas, tailless whipscorpions; Stewart, 1985; Stewart and Woolbright, Ms.).

Temperature. Temperature, as a factor influencing microhabitat use affected only subadults. Neither juveniles nor adults showed any difference between warm and cool nights in nocturnal perch height. Because temperature affected only subadults, it is not considered an important factor in microhabitat use among all three size classes.

Moisture. Changes in moisture conditions lead to significant differences in perch height of both juveniles and subadults. Both of these size classes were found higher on nights with wet rather than dry litter. Tent data reveal that juveniles and subadults were more active on wet nights than on dry nights. Although adults showed no significant change in perch height in response to moisture conditions,

they do respond to moisture in other ways. The numbers of frogs that climb into the canopy increases with the amount of moisture during a previous three-day period (Stewart, 1985), and calling activity by males is increased on wet nights (Woolbright, 1985). Another study has shown that adults respond to changing moisture conditions with postural changes (Pough et al., 1983); they found that frog postures on wet nights expose a maximum amount of the frog's surface area. As nights get progressively drier, the frog's change in posture exposes less and less of its surface. Frogs in the most water conserving posture expose 52% less surface area than those in high alert postures. So although adults show no significant differences in perch height between wet and dry nights, they do respond to changing moisture conditions with postural changes.

Ontogenetic shifts in microhabitat use occur in E. coqui. Of all the factors examined that could explain this, only one affected all three size classes - moisture conditions. Amphibians, with their permeable skin, are often constrained by moisture (Jameson et al., 1973). The greatest effect of moisture was on juveniles, less on subadults, and adults showed no perch height changes (except for those climbing into the canopy), but do show postural changes (Pough et al., 1983). This differential effect of moisture on the three size classes is not unexpected. Heatwole et al. (1969) found that juvenile E. coqui had a standard rate of moisture loss twice that of adults, even when activity levels and exposed surface area differences were controlled.

At El Verde the vegetation tends to dry quickly after rains, offering only isolated water-filled axils and bromeliad tanks as

rehydration sites. Both subadults and adults have been observed using these rehydration sites. The forest floor is always covered with a layer of fallen leaves, many curled. The litter offers a dense zone of rehydration sites consisting of wet surfaces and puddles in curled leaves and on rock surfaces. Perhaps juveniles are found low in the vegetation because they are at greatest risk of desiccation and cannot remain active far from reliable rehydration sites. As frogs get larger, the risk of dehydration may be reduced and therefore they can go farther before needing to rehydrate. When leaving the litter the frogs not only leave behind a dense supply of rehydration sites but they move up into a drier environment (Van Berkum et al., 1982). Pough et al. (1983) document the effects of water loss by adult frogs. They found that frogs in the canopy lost 20% more water than those in the understory. On wet nights frogs showed no significant change in water content yet on dry nights there was an 8% decrease in body water content. It is for the above reasons that I suggest moisture conditions are the major factor in microhabitat use among the three size classes of E. coqui.

Food as a Resource

Ontogenetic shifts in use of food were seen in E. coqui. Food type did not differ; all frogs ate predominately ants by numbers and by volume when only prey 0.5-3.0 mm in length were considered. Frogs did differ in the size of food eaten. As expected, juveniles ate the smallest prey (Mean = 1.4 mm), subadults ate larger prey (Mean = 1.8 mm) while adults took the largest prey (Mean = 4.1 mm). Neither

temperature nor moisture condition affected the mean length of prey eaten by any size class. The best explanation for differences in food use may be allometric differences in gape size among the three size classes. As gape size increases with increasing body size the size of prey that can be consumed increases as well (Emerson, 1985).

There is an interesting link between microhabitat and food use. As Table XI shows, the highest percentage of food items in the juvenile size range is found at ground level. Food in the subadult size range is found in highest abundance at 0-50 cm. Adult food items show no strong pattern. The highest percentage is found at 25 cm with the percentage fluctuating through the remaining height intervals. It could be that size classes are tracking their maximum-sized prey and are found perching where those prey are most abundant. If such is the case, food would be a factor responsible for microhabitat use. Alternatively, different size classes could simply be eating the prey found where they perch, in which case microhabitat would be a factor in food use. My data do not allow me to choose between these two hypotheses.

Finally, in addressing microhabitat and food use, I have looked for a single factor that could affect all three size classes. For microhabitat use, that factor was moisture, while for food it was gape size. But a factor does not have to affect all size classes to be important in causing differences in resource use. For example, reproductive behavior is a major factor in adult microhabitat selection. Adult males attract mates by calling from elevated perches (mean calling perch height of 93.5 cm; Townsend, 1984). Elevated perches have superior acoustic qualities (Narins and Hurley, 1982). So

males calling from elevated perches may attract more females. Males then lead females to nest sites (mean height of 30.5 cm; Townsend, 1984). Therefore both males and females climb into the vegetation to breed. While these behaviors are a very important aspect of adult microhabitat selection, they have no meaning for the other two size classes.

My study is the first to document ontogenetic shifts in resource use by a direct-developing frog. The most common resources examined in studies of intraspecific (ontogenetic shifts) or interspecific (resource partitioning) resource use are activity time, habitat, and food. Eleutherodactylus coqui shows ontogenetic changes in the use of microhabitat and food. The major factor responsible for microhabitat use in all size classes was most probably changing physiological tolerances to moisture conditions. As Toft (1985) found, more than one factor is responsible for the use of a resource. In E. coqui, mating behaviors are also a factor in microhabitat use for adults. Subadults are affected by temperature as well as moisture. Food size differed among the size classes primarily as a result of increasing gape size with increasing body size.

Ontogenetic shifts in resource use can be important when studying communities. Considering only the adults of the species in these studies may be misleading (Werner and Gilliam, 1984). Pre-adult organisms, although smaller, are far more numerous than adults. This pre-adult biomass has largely been ignored in the literature. As my study has shown, not all size classes of a species use resources in the same way (see also Schoener, 1970; Stewart and Martin, 1980; Simon

and Middendorf, 1976).

Fraser (1976a) found that two species of Plethodon salamanders partitioned resources differently depending on the size classes considered. Adults of the two species partition both habitat (cover objects) and food. Niche overlap for these resources is low and so coexistence is possible. Juvenile P. punctatus and adult P. hoffmani are similar in size and show wide overlap in the use of food and habitat. Fraser postulated that coexistence is possible for these size classes primarily because of non-coincident feeding. Therefore, while adults of the two species partition food and habitat, the smaller adults and larger juveniles do not.

In Fraser's (1976a) study, to have considered interactions among only adults would have resulted in an incomplete picture of the community dynamics. The same is true of the Eleutherodactylus community at El Verde. There, three species of Eleutherodactylus can all be found in the same habitat. Eleutherodactylus coqui is the largest and most numerous species with a maximum SVL of 55.0 mm; E. portoricensis is slightly smaller with a maximum SVL of 38.0 mm; E. wightmanae is smaller still at 20.0 mm SVL (Rivero, 1978). I have documented ontogenetic shifts in resource use by E. coqui. It seems likely that both E. portoricensis and E. wightmanae may also show changes in resource use with increasing SVL. Because of size (SVL) differences among adults, resource use may be very different. Yet if similar sized frogs are compared (e.g., adult E. wightmanae and subadult E. coqui), resource use could be similar. Consequently, to fully understand the use of resources by the Eleutherodactylus community at El Verde, all size classes should be considered.

Werner and Gilliam (1985) document ontogenetic shifts in resource use in a wide variety of organisms. Both urodeles and anurans with complex life cycles are represented. Frogs with complex life cycles have obvious ontogenetic shifts in resource use, that are well-described in the literature. This study for the first time documents these shifts in a direct-developing frog, E. coqui. Knowledge of ontogenetic shifts in resource use provides a more complete understanding of the life history of E. coqui. This knowledge, in turn, will lead to a greater understanding of the interactions of E. coqui within the anuran community of the Puerto Rican rain forest.

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