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Utilization of *Puya dasylirioides* (Bromeliaceae: Pitcairnoidea) as foraging site by *Bolitoglossa subpalmata* (Plethodontidae: Bolitoglossinii)

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Abstract: Foraging activities of *Bolitoglossa subpalmata* (Plethodontidae: Bolitoglossini) on *Puya dasylirioides* (Bromeliaceae: Pitcairnoidea) were studied at a peat bog on Cerro de la Muerte, Costa Rica. Salamanders climb bromeliad infructescences more often than other substrates, and several times during a single night, if weather conditions are favorable. Strong winds with high precipitation inhibited their surface activity. The animals showed a tendency to climb *Puya* with an intermediate degree of senescence where they actively prey on resident arthropods. Comparisons between number of ingested prey at the bromeliad against other substrates, suggest a better availability or a large number of prey at the infructescences. There was a low frequency of two or more salamanders climbing the same *Puya*. Sheltered microhabitats at the *Puya* and specific postures of the salamanders while foraging on the infructescences, enable long periods at the *Puya* without losing much water due to wind.

Key words: *Bolitoglossa subpalmata*, *Puya dasylirioides*, Salamander, forage, peat bog, Costa Rica.

More than a quarter of all species of tropical salamanders are *Bolitoglossa*, but many are poorly known (Wake 1993). For *Bolitoglossa subpalmata* Boulenger, few aspects of their natural history have been studyed so far (*e.g.* Vial 1968, Houck 1982, Ducey & Brodie 1983, Wake 1987, Brodie & Ducey 1991, Ducey & Brodie 1991, Ducey *et al.* 1993). Foraging strategies are unknown.

B. subpalmata is remarkable in habitat exploitation. It is considered a generalist that can be found -subject to favorable thermal and hydrical conditions- on terrestrial and arboreal habitats up to 30 m above the ground (Wake & Lynch 1976, Robinson 1977, Hanken *et al.* 1980, Wake 1987). This species is restricted to the Cordillera Central and the Cordillera de Talamanca of Costa Rica (Scott 1983). At the general vecinity of Cerro de la Muerte it occupies a wide range of altitudes with population densities among the highest known for any tropical plethodontid (Vial 1968). It is very abundant on local swampy depressions or peat bogs, where the terrestrial bromeliad *Puya dasylirioides* Standley -one of two species of *Puya* out of the Andes (Smith & Downs 1974)- also occurs in massive populations (Burt-Utley & Utley 1977).

On different occations, *B. subpalmata* was seen climbing the *Puya* infructescences during its nocturnal wanderings in the bog. These observations raised several questions about the reason for this behavior, which I explore in this article.

MATERIAL AND METHODS

Study site: The study was conducted from 1984 to 1985 on a raised ombotrophic bog at the Tres de Junio locality (2660 m.a.s.l.), 68 km from Cartago on the Interamerican Highway along the NW slope of Cerro de la Muerte massif (Fig. 1). The bog, approximately

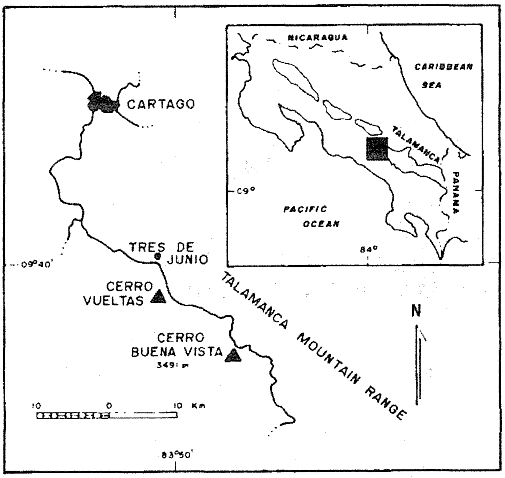

Fig. 1. Study site at Tres de Junio in the Cerro de la Muerte massif.

200 x 150 m, is located in a small depression along the road, surrounded by secondary growth oak montane forest and bisected by small streams. The vegetation is dominated in the center by dense clumps of *P. dasylirioides* growing upon a thick carpet of *Sphagnum spp.* (bogmoss), alternating with sedges, ferns and liverworths. At the bog's margin, ferns and grasses dominate the vegetation. Other bogs between Cerro Vueltas and Cerro Buena Vista (Fig. 1), also are inhabitated by large populations of *B. subpalmata* and *P. dasylirioides.*

Substrate preference: To determine on what substrate the salamanders preferentially performed its nocturnal activities, a 60 x 1 m EW transect across the bog was searched on five nights (3,17,18-V-84 and 4,5-VI-85). Numbers of salamanders were recorded at 20:00, 24:00 and 04:00 hr and classified by substrate categories: *Sphagnum*, *Puya* and other (*e.g.*, any kind of shrubs, live and dead *Blechnum* ferns). To avoid negative responses from salamanders, none were touched or illuminated more than five seconds. The position of the head and tail was noted with respect to the ground, wind direction and other salamanders. This procedure was followed along the study. Temperature and humidity conditions were measured at each observation time during the entire study, using a bulb thermometer and a commercial psychrometer (Schön, Germany). Precipitation was recorded at the Tres de Junio meteorological station about 20 m from the bog (Instituto Costarricense de Electricidad, unpublished data).

Activity on Puya: Salamander climbing behavior was assessed with regard to condition of the fruiting stalk of *Puya.* These conspicous structures result from reproductive meristerm bolting after flowering (Augspurger 1985). Depending on seed maturation and stalk senescence level, infructescences were classified into four subjective conditions, from condition 1, a green recently bolted meristerm, with or without flowers and a green rosette, to condition 4, a still upright stalk with fruit and bracts falling apart and a dark brown rosette. *Puya* from Cond.1 were absent from three surveys (20-X, 30-XII-84, 1-III-85), and when present not a single salamander was found. Therefore, Cond.1 is excluded from the calculations. On five nights (24-VIII, 20-X, 30-XII-84; 1-III, 5-VI-85) ten infructescences from each condition were randomly selected and tagged in the rosette within a set quadrat, 25 x 25 m, at the bog's centre. Numbers of salamanders on each infructescence were counted (excluding individuals out of the fruit-seed portion) at two hours intervals (20:00-22:00, 24:00-02:00 and 04:00-06:00 hr) and the same path of examination was followed.

Duration on infructescences: To estimate the time salamanders spent on the *Puya* infructescence, on two occasions (24-VIII, 20-X-84) five plants from each condition, containing one salamander just about to climb the first quarter of the fruit-seed portion of the stalk, were monitored over a period of five hours (maximum time spent on infructescences). Salamander presence was checked every hour; if absent, it was assumed they stayed the entire hour. In the few cases were another salamander climbed the same *Puya*, the subject was marked with a drop of dilute red ink placed on the salamander's back. Prior trials showed no obvious effects on the animal either from the diluted ink or the process of dropping it.

Foraging on Puya: Salamanders were collected (20-X-84, 20:00-21:00 hr) on the ground moss carpet (N=10), while climbing (N=10) and descending (22:00-23:00 hr, N=10) infructescences, to compare the amount of prey ingested in both substrates. The adult animals (>50 mm SV lenght, Vial 1968, Houck 1982) were anesthetized in a dilute solution of chloretone and preserved in 10% formalin. The stomachs were then washed and stored in 70% ethanol. Prey ingested was sorted with a microscope, counting all organisms greater than about 0.5 mm (visible at 10X power).

RESULTS

Substrate preference: Pooling together all surveys, salamanders were significantly more abundant on *Puya* (ANOVA, F=13.47, p<0.001) than any other substrate (Table 1).

TABLE 1

Average number of salamanders found on P. dasylirioides, Sphagnum *spp. and other substrats (shrubs, grasses, etc.), sorted by hour; combined data from five nights. Standard error in parenthesis*

Hour	*P. dasylirioides*	*Sphagnum* spp.	Other
20:00	17.4 (3.7)	4.8 (1.8)	2.2 (0.4)
24:00	12.6 (4.2)	3.4 (1.2)	2.0 (0.6)
04:00	2.0 (1.3)	1.8 (1.3)	0.6 (0.2)

The average number of animals was always higher in the infructescences regardless of the hour, and hence of the temperature and the relative humidity. Abundance on *Sphagnum* and other substrates was not significantly different from each other at the p<0.05 level [pair-wise comparisons of means (Tukey)]. Although salamander activity was not significantly different between dates (F=1.73, p>0.5), it varied between hours (F=6.74, p<0.005), with a minimum at 04:00 hr (Table 1, see further results). Almost all the salamanders observed were crawling between the bracts and fruits, head-up and on the wind-protected side of the infructescence (Fig.2). None seemed to passivily stay upon the infructesecence. Instead, it was clear they were actively exploring the crevices and spaces under and between adjacent fruits and bracts (Fig. 2), readly placing the head into cavities.

Activity on Puya: Salamander presence on *Puya* at different states of senescence (Cond.2,3,4) deviated significantly from random (X^2=40.50, df=2, p<0.001). It varied significantly with condition (F=52.89, p<0.001), showing Cond.3 with the highest average number of salamanders (9.7± SE=1.3) and percentage of bromeliads with salamanders on all dates (Fig. 3). Salamander activity on Cond.2 (3.9±1.0) and 4 (3.1±0.9) were not significantly different from each other at the p<0.05 level.

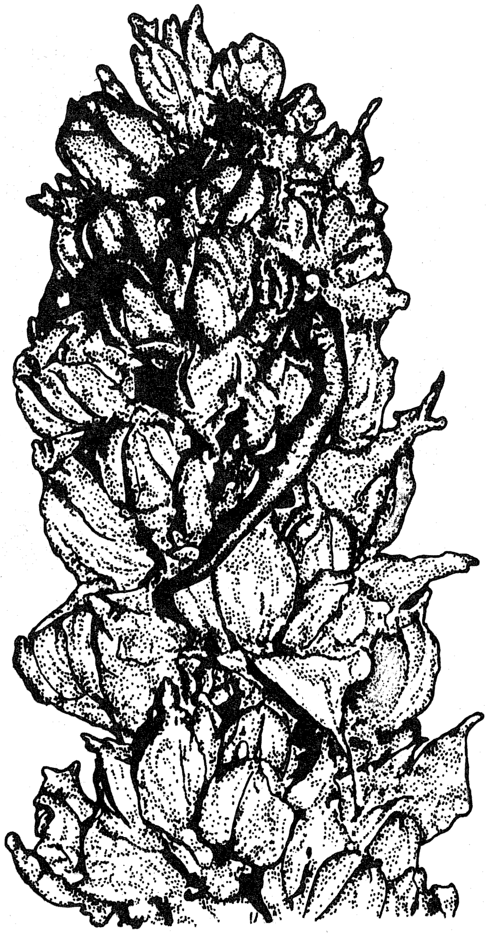

Fig. 2. *Bolitoglossa subpalmata* searching for prey on the wind protected side of a *Puya dasylirioides* infructescence; from a picture taken at the Tres de Junio bog, 30-XII-84, 23:00 hrs.

Following the percentage of active salamanders per condition, hour and date, the higher percentages are again exhibited by Cond.3. However, the trend when few animals were active (at the first hours and pre-dawn observations) is not as well defined as the midnight observations. For two dates (20-X-84, 1-III-85), the only active individuals were on Cond.2, nevertheless higher numbers of active salamanders were recorded on Cond.3 (N=10)

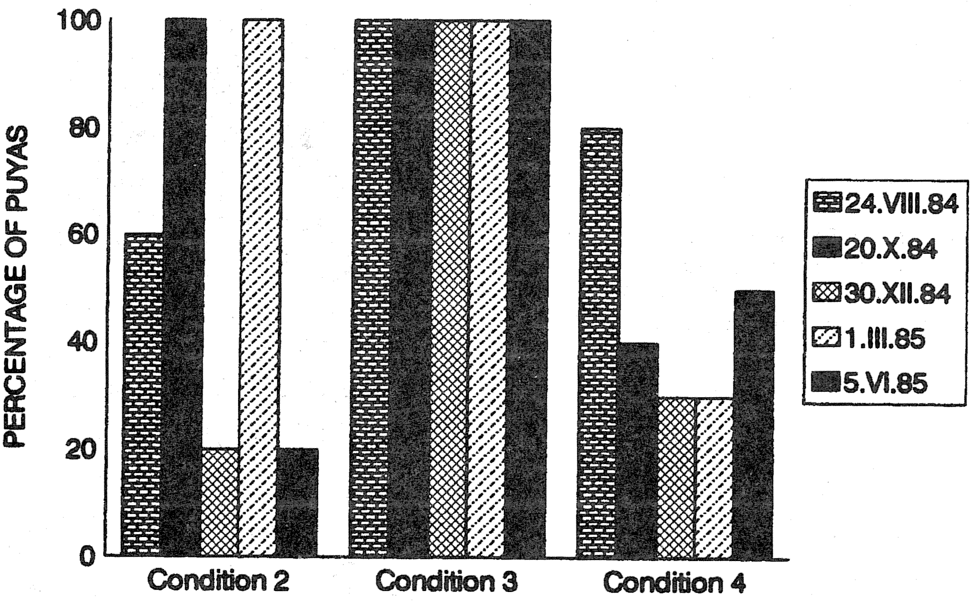

Fig. 3. Percentage of *Puya dasylirioides* with salamanders by infructescence condition and survey date.

than on Cond.2 (N=7), and the distribution differed from random (X^2=8.33, df=3, p<0.05).

Pooling together all the bromeliads from the entire study (N=150) at the maximum activity hour (20:00-22:00, Fig.3), 48.7% (N=73) had one salamander, 14% (N=21) two, 2% (N=3) three, 0.6% (N=1) four and 34.7% (N=52) none. The higher percentage of single salamanders climbing *Puya* remained throughout the night. Because no attempt was made to measure the animals to avoid disturbing them, the proportion of adults or juveniles using the plant is not known. No individual under about 30 mm SVL was seen. When more than one salamander climbed the infructescence, usually the larger animals tended to be at the upper portion of the stalk, and separated from the other. However in the only case of four individuals together on the same infructescence, three were clustered at one side, displaying the posture cited before (Fig.2).

Overall, salamander activity within the quadrat varied significantly with the date (F=9.92, p<0.001) and hour (F=62.05, p<0.001); contrasting with the non-significance of the substrate preference study (see before). For a pairwise comparison of means, dates 30-XII-84 and 5-VI-85 are significantly different from the rest. The activity closely matches the environmental conditions prevailing during the study. Nights with less surface activity (30-XII-84, 5-VI-85, Fig.3) are from months with lower and higher average precipitation (Fig.4), and these were the nights with lower temperature and strong wind conditions. The driest month of the study, March 1985 (Fig.4), had a lower salamander surface activity, but it was not significantly different from moderate rainy and humid months.

Duration on infructescences: Salamanders tended to stay longer on *Puya* from Cond.3 (F=25.88, p<0.001), independently from night of observation (F=1.68, 0.05<p<0.5, Table 2). Permanence on other conditions was not significantly different. When two salamanders were at the same Plant (three cases), none seemed reactive to the others .

Foraging on Puya: Eight different taxa, mainly insects, were found in the stomach contents of the salamanders (Table 3), and descending animals had a higher number of prey (F=12.18, p<0.001). The number of prey of salamanders on the ground and conspecifics ready to climb where not significantly different.

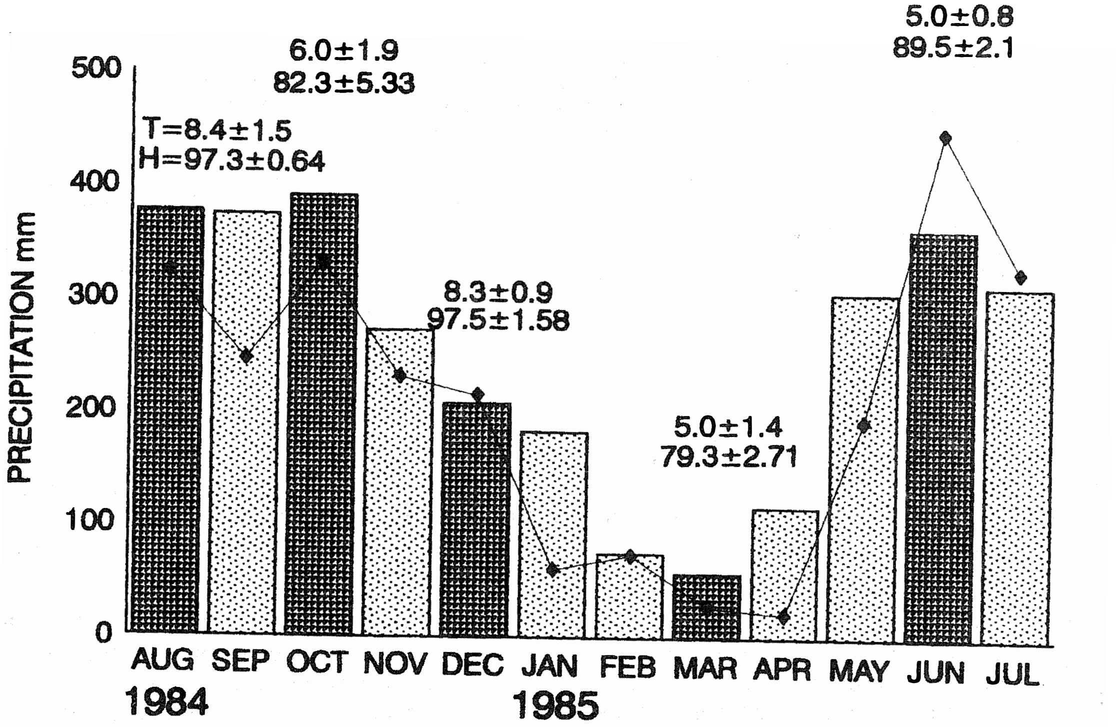

Fig. 4. Atmospheric data at the Tres de Junio bog. T= temperature (^{o}C) ± standard error; H= humidity (%); bars monthly average precipitation (mm), 1962-1989; line monthly average precipitation during the study.

TABLE 2

Average time (hr) spent by salamanders on Puya in two nights, sorted by plant condition. (see text). Standard error in parenthesis

Condition	24-VIII-1984	20-X-1984
1	No activity	No activity
2	1.4 (0.2)	1.6 (0.4)
3	2.4 (0.5)	3.4 (0.5)
4	1.2 (0.2)	1.0

DISCUSSION

The occurrence of *B. subpalmata* on epiphytic bromeliads is related with foraging (Hanken *et al.* 1980). This plant climbing behavior (expansion of range) to increase prey capture, has been noted in other plethodontids as well (Cunningham 1960, Wake & Lynch 1976, Jaeger 1978). The increase in salamander mobility while expanding its foraging range increases prey capture (Fraser 1976). Thus, for the *B. subpalmata* bog population, a preference to climb *Puya*, rather than wandering over other substrates, is related to an increase of prey ingestion. The significantly higher prey number in climbing salamanders may be an indication of its availability on the infructescenses. Litter arthropod densities vary drastically within a year, depending on weather conditions and substrate heterogeneity (Levins & Windsor 1990, Nadkarni & Longino 1990, Frith & Frith 1990). Therefore, vegetation is a food source more readily available to salamanders than litter (Jaeger 1978). Decaying vegetation could harbour considerable arthropod populations (Frith & Frith 1990). Decomposition rates are low in *Sphagnum* bogs (Johnson *et al.* 1990), perhaps limiting ground dwelling arthropods that flourish on decaying organic material. For this reason, the salamanders climb and stay longer on decaying infructescences with enough organic material attached to the stalk.

B. subpalmata seems to be able to descriminate which *Puya* will be climbed. This could be done by trial and error, or by chemical cues at

TABLE 3

Number of individuals per taxa of prey ingested by salamanders collected on the ground (20:00-21:00 hrs, N=10 salamanders), while ascending (20:00-21:00 hrs, N=10) and descending (22:00-23:00 hrs, N=10) P. dasyliriodes *infrutescences*

Taxa	Ground	Ascending	Descending
Isoptera	4	3	3
Ortoptera	5	4	5
Diptera	2	2	7
Lepidoptera	0	10	14
Hymenoptera	1	0	0
Aranea	1	4	7
Coleoptera	3	6	16
Nematoda*	7	3	5
Total	23	34	57

(*) There is no certainty if they were ingested prey or parasites, therefore these are excluded from calculations.

the bromeliad rosette, possibly by following a gradient of prey density (Jaeger 1978) or a combination of the latter with chemical cues.

Large numbers of plant dwelling insects at high elevations are common during the dry season (Janzen 1973). Perhaps this explains the high salamander activity on *Puya* during the driest month. Salamanders' surface activity is limited by body water loss to the air (Feder 1982a,b, Feder & Lynch 1982), so climate restricts foraging time (Feder 1983). Considering this, *Puya* must be an excelent food resource, since the surface activity is reduced and prey location is maximized.

Because ingested prey could remain in a salamander digestive tract 2-4 days (Maiorana 1978, Jaeger & Bernard 1981), stomach contents of the salamanders captured before climbing could be both prey ingested at the ground or the previous nights at the bromeliad. No marking of salamanders was done, so I was unable to determine how often the same individual climbs an individual *Puya*. The latter is important because previous studies had found that a small portion of the entire salamander population surfaces at a given night (Vial 1968, Fraser 1976, Jaeger 1981, Feder & Lynch 1982). It is therefore not surprising to find individuals who use the *Puya* consistently as has been reported for other salamanders exploiting a food resource (see Cunningham 1960, Jaeger 1980b, 1981) . Nevertheless, this situation needs more detailed studies to clarify why some individuals do not surface while others do, and hence, ingest more prey on the bromeliad.

Plethodontids show several mechanisms for prey detection such as vision, olfaction, vibration sense and chemorreception (David & Jaeger 1981, Houck & Verrell 1993, Jaeger & Forester 1993). The searching behavior of *B. subpalmata* indicates that prey location is determined by visual and perhaps chemical cues. Bolitoglossines are considered the extreme of prey capture specialization among plethodontids (Roth & Schmidt 1993), combining their excellent visual capabilities with a projectile tongue.

The long period of surface activity observed here, possibly an overestimation, contrasts with Vial's (1968) report. He found no surface activity longer than four hours. Perhaps the observed behavior at the *Puya* enables the salamander to stay longer. Crawling among the fruits and bracts on the wind protected side, the animal stays within the boundary of still air next to the structures, thus avoiding high convective water loss. A similar situation is considered to happen very close to the ground (Miller 1991), but not on exposed vegetation (Feder 1983). These sheltered microhabitats have been reported elsewhere for Long-lived rossette plants, depending on pubescence degree (Miller 1986) and layer thickness of the dead leaves still attached to the stem (Goldstein & Meinzer 1983).

The rarity of co-occupancy could be an indication of antagonistic behavior; perhaps there is a territorial defense of foraging sites (infructescences) for mating, as suggested by Mathis (1991) for *Plethodon cinereus.*

Plethodontid life histories vary considerably (Houck 1977, Tilley & Bernardo 1993), and it will be of interest to find out if the relationship reported here occurs in other bogs of the Talamanca range (*e.g.* Cerro Kámuk) where *B. subpalmata* and *P. dasylirioides* coexist.

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RESUMEN

En una turbera del Cerro de la Muerte, Costa Rica, se estudió la actividad alimenticia de *Bolitoglossa subpalmata* (Plethodontidae: Bolitoglossini) en *Puya Dasylirioides* (Bromeliaceae: Pitcairnoidea). Las salamandras subieron a las inflorescencias de las bromelias con mayor frecuencia que a otros sustratos, durante varios períodos en la noche si las condiciones climáticas eran favorables. Los vientos fuertes, junto con una alta precipitación, inhiben la actividad de la salamandra, que mostró una tendencia a subir plantas de mediana edad, donde depredan activamente en los artrópodos. Las comparaciones del número de presas ingeridas en la bromelia con respecto a otros sustratos, sugieren que en la primera hay una mayor disponibilidad . Fue poco frecuente la presencia de dos o más salamandras en una misma infructescencia. Los microambientes protegidos de *Puya* junto con posturas específicas de la salamandra durante la alimentación en la infructescencia, le permiten permanecer por largos períodos en la bromelia sin perder mucha agua por efecto del viento.

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Postscript

On July 15 and 16, 1994, the Tres de Junio bog was visited at night time (20:00-22:00hr). In spite of the appropiate weather conditions during our survey, no salamanders were seen climbing *Puya* infructescence. At a nearby bog, 74 plants were inspected and only two juvenile salamanders (<40 mm SVL) climbed the stalk. Surprisinly, the smaller one was on a *Puya* Cond. 1; the other upon Cond. 4.