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Effects of climate on inflorescences of the aroid (Araceae) Xanthosoma sp. and visitation rates of their scarab beetle pollinators, Cyclocephala sp.

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ABSTRACT

Spadices of many aroids (Araceae) go through a process known as "thermogenesis", manufacturing heat to attract scarab (Coleoptera) pollinators. In Monteverde, Puntarenas, Costa Rica, *Xanthosoma undipes* occurs in patches at 1550 meters elevation. Here they attract two scarabs that are thought to be the sole pollinators: *Cyclocephala nigerrima* and *C. sexpunctata.* Chances of successful pollination of *Xanthosoma* have been shown to increase drastically with higher visitation rates of scarabs. Previous studies in Monteverde found no relationship between the temperature of the spathe and beetle visitation (Craig 2001) though taller plants at lower altitudes have been shown to attract more beetles (Sica 1999). Here, I examine beetle visitation to *Xanthosoma* in more detail by examining plant dispersion, plant cover, spathe/spadix characteristics, and weather. In total I observed 231 beetles for a mean of 4.1 ± 5.2 per inflorescence. Sixty-two percent were *C. nigerrima.* A low recapture rate (4%) suggests wide ranging populations of both species. Visitation to inflorescences was greatest for plant under tree cover, with large spathe openings, and shorter, warmer spadices. In addition, warmer nights had higher rates of beetle visitation, resulting in more beetles per inflorescence. Therefore, beetle visitation to Xanthosoma is dependant upon a combination of plant cover, spathe/spadix morphology and weather. Microhabitat preferences, ability to find active inflorescences, and warmer temperatures suggest that *X. undipes* must accommodate to scarab behavior to insure visitation and pollination.

RESUMEN

Los espádices de muchos araceas (Araceae) muestran un proceso que se llama termogénesis, produciendo calor para atraer escarabajos polinizadores. En Monteverde, Puntarenas, Costa Rica, *Xanthosoma undipes* ocurre en parches a 1550 metros de elevación. Aquí, atraen dos especies de escarabajos polinizadores: *Cyclocephala nigerrima y C. sexpunctata.* Cambios en el éxito de la polinización de *Xanthosoma undipes* ha mostrado que aumenta drásticamente al subir la proporción de visitas de los escarabajos. Estudios realizados en Monteverde no mostraron una relación entre la temperatura de la espata y el número de visitas de los escarabajos, sin embargo, plantas más altas que están en elevaciones bajas han mostrado atraer más escarabajos (Sica 1999). En este estudio se examinó la visitación de los escarabajos en *Xanthosoma undipes* en mas detalle, al tomar en consideración la dispersión de las plantas, la cubierta de las plantas (espádice/espata) y el clima. En total, observe 231 escarabajos con un promedio de 4.1 ± *5.2* en cada flor. *Cyclocephala nigerrima* se presentó en un 62% de los escarabajos. El porcentaje de recaptura fue baja (4%) y esto sugiere que hay un alcance amplio de las dos especies de escarabajos. La visita a las flores fue mayor para las plantas que estuvieron bajo la cubierta de los árboles y con las aberturas más grandes de las espatas y los espádices más cortos y más calientes. También se encontro mas visitas de los escarabajos en las noches calientes y había mas escarabajos por flor. Por eso, las visitas de los escarabajos en *Xanthosoma undipes* depende de la cobertura sobre las plantas, la morfología de las plantas y el clima.

Introduction

Xanthosoma spp. and other aroids (Araceae), use thermogenetic heating of their male spadices in order to attract scarab beetle pollinators. For these species, the spathe covers the spadix, constricting to form a kettle at the bottom (see figure 1). Female flowers on the spadix are enclosed by the kettle while male flowers above are exposed as the spathe opens. This occurs only on the first night of thermogenesis, as scarabs first arrive, and the second and final night of heat production, when male flowers are releasing pollen that beetles withdraw while leaving (Goldwasser 1987). Apparently, beetles are attracted to inflorescences only on the first night of activity during and after heating. It is believed heat is used to further volatize odors that are capable of attracting beetles from long distances (Gottsberger and Silberbauer-Gottsberger 1991). Once near the inflorescence, beetles recognize the white spathe/spadix visually and fly to it, landing on it and crawling into the kettle to feed and copulate.

Factors influencing the attraction of scarabs to aroids have been studied for *Xantosoma undipes* and its two scarab pollinators: *Cyclocephala nigerrima,* a black species endemic to Costa Rica typically found from 1300 to 1700 m elevation and *C. sexpunctata*, a light brown species with chestnut spots that is common from Mexico to Bolivia that is usually found from zero to 1500 m elevation (Goldwasser 1987). Visitation by these scarabs is vital to pollination of the plant, with chances of fruit set increasing exponentially with the first few incoming beetles (Goldwasser 1987). Spadix temperatures range from 36° to 46°C but apparently temperature is a poor indicator of the number of beetles an inflorescence will attract (Craig 2001). Likewise, spadix and spathe size do not seem to affect beetle visitation (Craig 2001) though taller plants may draw more beetles (Sica 1999). Beetle are known to commonly travel several kilometers in a night (Goldwasser 1987), and this may be why clumps of plants attract lower rates of beetles per inflorescence, as the number of beetles within a certain range of attraction are divided among more spathes (Sica 1999). Weather may affect visitation rates on a day to day basis, as low temperatures have been observed to inhibit flying abilities for pollinating scarabs (Gottsberger and Silberbauer-Gottsberger 1991). In support of this, higher rates of visitation among beetles occur at lower altitudes, where temperatures are generally higher (Sica 1999) in comparison to upper elevations. On seasonal time scale, visitation rates within the tropics depend upon patterns of beetle abundances that are shown to increase with litter moisture (Levings and Windsor 1984) and are dependent on the "magnitudes" of wet and dry seasons (Denlinger 1980).

In this study I attempt to understand the nature of *Cyclocephala* attraction to *X. undipes* more entirely. I examine the role plant dispersal may play on beetles that are known only to live within spathes and travel from plant to plant. I also examine attributes of the spathe/spadix that may increase their attractiveness either in scent, like spadix height and size of the spathe opening, or visually, such as size of the spathe and the angle it may present itself to an incoming beetle. Because plants occur along forest edge, under pasture trees, or open sky and the final "honing in on" the spathe is done visually (Gottsberger and Silberbauer-Gottsberger 1991), whether an inflorescence is covered by a *Xanthosoma* leaf, tree, or sky may influence beetle preferences. Finally, low ambient temperatures and rainfall may inhibit beetle visitation by affecting flight ability and metabolic levels (Gottsberger and Silberbauer-Gottsberger 1991).

METHODS

Field work was conducted during the transition from wet season to dry season, from October 25th to November 15th, 2001 in the Monteverde region, Costa Rica. The study area was a large field around 1550 m elevation about 1 km west of Skywalk/Sky trek. *Xanthosoma sp.* covered many parts of the field, including in open pasture, underneath canopy trees dispersed sparsely throughout the field, and along edges where the field merged into continuous forest.

The entire pasture was examined during each day of the study. Only *X. undipes* with active inflorescences were examined for data and the number of beetle individuals were noted. Inflorescences after the first night of activity can be distinguished by a partially open spathe that is pure white with minimal spotting, by the presence of insects including Muridae, Aphidae, and Diptera, and possibly by scarabs. After the second night of activity male florets release pollen, making differentiation between these stages clear. In circumstances where it was not clear if the inflorescence had yet become activate there were never scarabs present. In these cases the inflorescence was marked, and measurements were made the next day using male florets as indicators of activity.

Spathes in the studied patch sometimes had a vertical path from the sky blocked by either a leaf of *X. undipes* or one of the many canopy trees at the site. Thus, each spathe/spadix was placed into the category of either tree coverage, *X. undipes* leaf coverage, or no coverage. In cases where a spathe was covered by a leaf as well as another *X. undipes,* the latter was category given because it was usually less than a meter away from the spathe versus the several meters away that tree cover usually was.

Characteristics of spatial dispersions and vegetative morphological characteristics were measured using a tape measure. For each plant the nearest neighbor of *X. undipes* was measured by recording the distance to the nearest *X. undipes.* Distance to the nearest *X. undipes* with an active spadices was measured for an idea of spatial dispersion of activity. For every plant in which data was collected, the height from the ground to the base of the leaf stems was measured, as was the circumference of the stalk at 20 cm from the ground. The number of leaves attached to each observed plant was also recorded.

The following morphological characteristics of the spathe/spadix were measured using a ruler: the size of the horizontal opening in the spathe at the widest point (cm), the length of the hood and kettle (cm), and the lengths of both the male and female segments of the spadix (cm) (Appendix A). The angle that the spathe bent over was measured by aligning a protractor that had a pendulum attached to it from the side of the spathe so that one edge touched the tip of the hood and the other pointed towards the center of the kettle.

J. A. Pounds collected weather data at the nearby Monteverde Cloud Forest Preserve, which is at a similar altitude and is also considered Lower Montane Wet Forest. He provided a list of daily rainfall (cm), as well and daily maximum and minimum temperatures (°C).

The number of individuals of C. nigerrima and C. sexpunctata observed in each spathe for which data was collected was recorded. Mark and recapture began on October 29 and lasted until the end of the study on November 13th. To do this part of the study any observed beetles were removed from within the spathe, usually requiring the overlapping portion of the kettle to be pulled apart. Once in hand a dot of liquid correction fluid was placed on the thorax of each captured beetle. Beetles were then placed back into the spathe although some became disturbed and left, either dropping and burrowing into the ground litter or flying away to a nearby tree. Once marking began scarab individuals exhibiting this “white dot” were recorded for each observed spathe/spadix.

Results

Effects of cover on scarab visitation rates

Whether spathes occurred under open sky, leaves of other X. unipes or canopy sized trees influenced the number of beetles visiting that plant (1WAY ANOVA, p = 0.024 for total beetles). Spathes on plants below trees had an average of 5.8 ± 5.9 beetles per inflorescence while plants below leaves showed 2.9 ± 2.4 and spathes under open skies showed 1.9 ± 2.5. Note that in all cases standard deviation was high. Many plants had no scarabs (2 of 12 for tree cover; 4 of 16 for leaf cover; 7 of 23 for open sky). Maximum beetle number recorded with cover measured was 16, and occurred under a canopy tree.

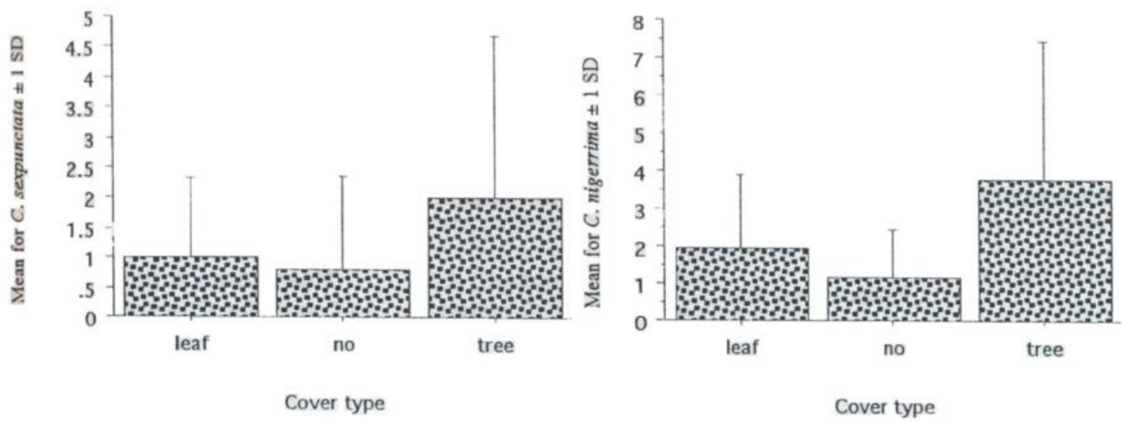

Figure 1. Bar charts for mean number scarabs within an inflorescence under different types of cover. Both species recorded higher average means under tree cover (C. nigerrima; p. = 0.0115, f = 4.940: C, sexpunctata; p = .2195, f = 1.569).

Effects of spatial dispersion on scarab visitation rates

The "tightness" in which plants were clumped together did not influence number of beetles visiting that plant (Table 1). There was not much variation in distance between plants as most were separated by less than one meter (0.86 ± 0.60m). Distances between active spadices within this patch were more varied (33.37 ± 36.41m) but the distance of separation between these odor-releasing spadices did not influence the number of beetles that visited (Table 1).

TABLE 1. Results of regressions of numbers of scarab individual s per species versus mean "nearest neighbor" distances. "Nearest neighbors" consisted of the nearest plant (cm), and the nearest active plant (m). Nearest neighbor distances did not have an effect on the number of scarabs found in spathes.

		C. nigerrima			C. sexpunctata	
Dispersal Distances	P-Value	R Squared	Count	P-Value	R Squared	Count
Nearest Xanthosoma sp.	0.28	0.02	56	0.52	0.01	56
Nearest Active Xanthosoma sp.	0.58	0.01	40	0.54	0.01	40

TABLE 2. Results of Unpaired t-tests between C. nigerrima and C. sexpunctata for dispersals of Xanthosoma sp. Independent variables include distance to the nearest Xanthosoma sp. (cm) and distance to the nearest Xanthosoma sp. With an inflorescence between nights of activity (m). There was no difference between the species for wither of these measurements of dispersal.

Dispersal Factor	P-Value	t - value	Mean distance (m) ± SD (Count) for C. nigerrima	Mean distance (m) ± SD (Count for C. sexpunctata
Nearest Plant	0.95	-0.05	96.60 ±49.96 (143)	96.98 ± 58.19 (87)
Nearest Active Plant	0.32	-0.99	0.29 ±0.37 (63)	0.38 ±0.47 (36)

Effects of vegetative characteristics on scarab visitation rates

A plant's size was a poor indicator of scarab visitation rates (Table 3). Plants producing inflorescences had a mean height of 120 ± 41 cm and a mean circumference of 46 ± 9 cm. There were a mean of 2.6 leaves for all observed plants. No plants were found that had more than four leaves or less than one.

TABLE 3. Results of regressions of numbers of scarab individuals the size of measured vegetative characteristics. Characteristics include number of leaves, height to base of leaves (cm), and circumference 20 cm from the bass (cm). No vegetative traits were found to influence rates of scarab visitation.

		C. nigerrima			C. sexpunctata	
Vegetative Characteristics	P-Value	R Squared	Count	P-Value	R Squared	Count
leaves	0.89	<0.01	56	0.61	<0.01	56
height	0.52	<0.01	56	0.64	<0.01	56
Circumference	0.20	0.03	56	0.93	<0.01	56

TABLE 4. Results of Unpaired t-tests between C. nigerrima and C. sexpunctata for measured vegetative characteristics. Independent variables include number of leaves, height (cm), and circumference (cm).

Characteristics of Inflorescences	P-Value	t-value	Mean ± SD (Count) for C. nigerrima	Mean ± SD (Count) for C. sexpunctata
leaves	0.30	1.03	2.44 ± 0.6 (92)	2.34 ± 0.58 (53)
height	0.78	0.28	116.14 ± 35.66 (143)	114.70 ± 32.71 (87)
circumference	0.18	-1.34	45.03 ± 9.25 (143)	46.75 ± 9.61 (87)

Effects of spathe/spadix morphological characteristics on scarab visitation

More open spathes with smaller male spadices had more beetles and were preferred by *C. nigerrima* (Tables 5, 6). Visitation of *C. nigerrima* was more frequent in plants with smaller hoods, and a smaller spathe structure was also favored by this species than by *C. sexpunctata* (Tables 5, 6). *Cyclocephala sexpunctata* were found to occur with more frequency as spathes bent over less spathes (Table 5), and also preferred less bent over spathes than *C. nigerrima* (Tables 5, 6).

TABLE 5. Results of regressions of numbers of scarab individuals versus measured characteristics of inflorescences. Characteristics include spathe opening (cm), spathe angle, length of hood (cm), length of the hood and kettle together (cm), length of the male spadix (cm), and length of the female spadix (cm). *Cyclocephala nigerrima* tended to have increased rates of visitations for larger spathe openings and smaller male spadices.

Inflorescence Characteristics	C. nigerrima			C. sexpunctata		
	P-Value	R Squared	Count	P-Value	R Squared	Count
spathe opening	0.04	0.14	29	0.56	0.01	29
spathe angle	0.58	<0.01	48	0.06	0.07	48
length of hood	0.05	0.07	56	0.86	<0.01	56
length of hood + kettle	0.13	0.04	56	0.7	0.03	56
length of male spadix	0.04	0.08	56	0.96	<0.01	56
length of female spadix	0.13	0.05	44	0.72	0.03	44

TABLE 6. Results of Unpaired t-tests between C. nigerrima and C. sexpunctata for measured characteristics of inflorescences. Independent variables include spathe opening (cm), spathe angle, length of hood (cm), length of the hood and kettle together (cm), length of the male spadix (cm), and length of the female spadix (cm). Significant differences were found for spathe opening, spathe angle, and length of hood and kettle together.

Characteristics of Inflorescences	P-Value	t-value	Mean ± SD (Count) for C. nigerrima	Mean ± SD (Count) for C. sexpunctata
spathe opening	0.04	2.13	2.89 ± 2.33 (39)	1.78 ± 1.08
spathe angle	0.05	1.98	15.85 ± 8.68 (92)	13.11 ± 6.67 (53)
length of hood	0.20	-1.27	16.55 ± .54 (143)	17.02 ± 3.00 (87)
length of hood + kettle	0.04	-2.05	24.15 ± 3.11 (143)	25.09 ± 3.73 (87)
length of male spadix	0.07	-1.81	14.62 ± 2.04 (143)	15.13 ± 2.05 (87)
length of female spadix	0.76	0.30	3.56 ± 0.47 (73)	3.53 ± 0.55 (46)

Effects of weather on beetle visitation and spathe/spadix morphology

Rainfall as well as daily maximum and minimum temperatures influenced both spathe morphology and the number of visiting scarabs. The weather data encompassed a wide range as it was recorded during the transition from the wet season to the windy-misty, with temporal occurring in the middle of the study. Rainfall ranged from 0.1 to 36.1 cm (mean = 10.3 ± 11.8 cm). The highest temperature recorded was 21.5°C (mean daily maximum temperature = 19.9 ± 0.9°C) and the lowest recorded temperature was 14°C (mean daily minimum temperature = 15.5 ± 0.9°C). Higher daily maximum temperatures increased beetle numbers of both species as did higher daily minimum temperatures for *C. nigerrima* (Table 7). The beetle species do not clearly prefer different weather conditions for visitation (Table 8), although there are differences between the beetle species in their preferences of the size of the spathe opening and the angle at which it is bent over (Table 5) – both being traits of the spathe that are influenced by weather (Table 9). Spathes opened more at higher temperatures (Table 9), and although there were no differences in temperature preferences of the beetles for visitation *C. nigerrima* was found to prefer more open spathes than *C. sexpunctata*. Another case of a temperature-dependent trait of a spathe that has different preferences between species is with the angle at which the spathe bends over, which was found to bend more after higher maximum temperatures and more rain. Again, more bent over spathes were found to be preferred more by *C. nigerrima*. Thus, even though beetle species did not demonstrate different preferences in their visitations due to temperature alone, they did show differences in preferences based on spathe characteristics that were themselves dependent on temperature. Furthermore, *C. nigerrima*, the highland species, preferred spathe characteristics that increased in magnitude at higher temperatures.

TABLE 7. Summary of regressions between numbers of scarab individuals found per inflorescence variables measured on the previous day. Rainfall (cm), daily maximum (°C) and daily minimum (°C) are included. Scarabs visited at higher frequencies when temperatures were higher.

Weather Factors	C. nigerrima			C. sexpunctata		
	P-Value	R Squared	Count	P-Value	R Squared	Count
Rain	0.13	0.04	56	0.28	0.02	56
previous max. temp.	<0.01	0.24	56	0.02	0.10	56
previous min. temp.	<0.01	0.20	56	0.11	0.05	56

TABLE 8. Results of Unpaired t-tests between C. nigerrima and C. sexpunctata for dispersals for effects of weather during the previous day and night. Independent variables include daily rainfall (cm), previous maximum temperature (°C), and previous minimum temperature (°C). There are no clear differences between the two species in regards to weather factors for individuals studied.

Dispersal Factor	P-Value	t-value	Mean ± SD (Count) for C. nigerrima	Mean ± SD (Count) for C. sexpunctata
Rain	0.08	0.33	7.63 ± 9.92(143)	7.16 ± 10.90 (86)
Maximum	0.64	-0.47	20.40 ± 0.90 (143)	20.47 ± 1.08 (86)
Minimum	0.62	0.49	15.91 ± 0.66 (143)	15.86 ± 0.75 (86)

TABLE 9. Summary of regressions of spathe opening (cm) and spathe angle versus rain (cm), previous daily maximum temperature (°C), and previous daily minimum temperature (°C). Spathe openings increased with temperature. Spathes became more vertical at higher temperatures and bent over more with increasing rain.

Weather Factors	Spathe Opening			Spathe Angle		
	P-Value	R Squared	Count	P-Value	R Squared	Count
Rain	0.55	0.01	29	<0.01	0.2	56
previous max. temp.	0.03	0.16	29	0.01	0.16	48
previous min. temp.	0.03	0.16	29	0.94	<0.01	48

Census of the visiting scarabs

A total of 231 beetles were observed (mean = 4.1; SD = 2.9; n = 57). Of these 143 (62%) were *C. nigerrima*, and 88 (38%) were *C. sexpunctata*. Beginning October 29, 101 scarabs were marked. Only four (4%) were recaptured over the course of the study.

DISCUSSION

Scarab visitation to *X. undipes* is affected by a combination of plant overstory, spathe/spadix characteristics and climate. There are diverse biological explanations for how each of these factors may affect the final rate of beetle visitation in conjunction with one another. These explanations generally describe factors affecting the size of a plants odor plume and olfactory perception of the spathe/spadix by the scarab, visual recognition of the spathe/spadix, flying ability, or origin of the scarabs journey.

More scarabs are found under tree cover that may provide a blockage from wind and rain, creating a scent trail that is easier to follow and also making it easier to see the spathe. The trees within the study sight were large and oftentimes covered in epiphytes –including aroids. It is possible that some of the beetles came from out of the trees as many of the beetles that were disturbed in handling flew into a nearby tree and remained there. Aroid spathe/spadices provide all the basic life requirements for the scarab; food shelter and a congregation place for copulation (Goldwasser 1987), so it is probable that if some of the beetles are coming out of overhanging trees it may actually be the epiphytic aroids within them that they are staying.

More beetles were found inside of spathes on warmer nights, which may increase volatility of olfactory compounds and also allow beetles to be more active. Temperature is known to have effects on the foraging patterns and energetics of insects, with activity generally decreasing at lower temperatures (Armbruster and Berg, 1994). Low temperatures decrease flying ability among insects in general (Martinez del Rio and Burquez 1986) and also seem to inhibit the flying ability of beetles specific to avoid pollination (Gottsberger and Silbauer-Gottsberger (1991). Higher temperatures and wind are both thought to increase plume size of odors although climatic factors may have a more profound influence on the physical nature of foraging insects (Armbruster and Berg 1994).

Inflorescences with larger spathe openings, larger hoods, and shorter male spadices attracted more *C. nigerrima,* and may relate to a plants ability to spread its attractive scent more effectively. More *C. nigerrima* were also found in spathes that were more bent over, possibly because the spathe openings were better covered by the back of the spathe from rain, or because this would increase their visibility from above. More open spathes could release scent more effectively because they have a smaller barrier to diffusion of scented compounds and provide more space for air currents to enter the spathe. It is unlikely that the size of the spathe opening is related to the ability of a beetle to enter because scarabs are easily strong enough to wedge through the two pieces of the spathe. Beetles were found in some spathes that were not open but had begun to "loosen". Shorter male spadices are known to produce more heat (Craig 2001), and although higher spathe temperatures are not known to be more attractive to *C. sexpunctata* (Craig 2001) they may be to *C. nigerrima,* the species which higher rates of visitation were noted in plants with shorter male spadices. Larger hoods probably are easier for the beetles to recognize visually, important as the beetles near the end of their search for the active spathe.

The two beetle species responded differently to some morphological traits in the spathes. *Cyclocephala nigerrima* was found in more open, smaller spathes that were bent over more than those in which *C. sexpunctata* was found. While the degree of "openness" a spathe possesses may affect its olfactory attraction to scarabs, spathe size is probably more important in visual recognition. Thus, it is possible that *C. nigerrima* relies more on olfactory cues than *C. sexpunctata* to find active spathes, while C. *sexpunctata* may have superior sight. Because at close range the attraction to the inflorescence is based on visual recognition, when distances between active inflorescences are small, plants that have spathes that are more advantageous visually may draw more beetles from the "pool" of odor surrounding the patch. When distances between active spadices are greater the importance of the strength of the scent an individual plant may increase. It is possible that the levels of importance olfactory and visual characteristics are to beetle visitation may vary by species.

Neither plant size, nor dispersion of plants affected scarab visitation rates. That plant size did not influence scarab visitation is consistent with Craig's (2001) study, but contradicts Sica's (1999) study finding higher visitation rates in taller plants. Larger plants have been found to have larger spathe/spadices (Craig 2001). Any relation a plant's size has to beetle visitation is probably through its relation to sizes of its spathe/spadix characteristics, the center of the interaction between the plant and scarab. Neither nearest neighbor distance of plants, nor plants with receptive spadices had an effect on beetle visitation. Patches with multiple inflorescences should have larger odor plumes, with concentrations of odoriferous substances detectable at further distances both radially and linearly (as pushed by the wind). The benefits of larger odor plumes could be limited by the flight limitations of the scarabs, or simply by the patchy distribution of beetle populations limited to light-gap plants that grow in clumps. Larger odor plumes are more likely to, but do not necessarily spread to more patches where beetles occur.

The mark and recapture experiment, which yielded a total recapture rate of only 4% over two weeks, suggests that the majority of these local scarab populations extend beyond the mega patch of *Xanthosoma sp.* studied. Scarabs are able to fly at least a kilometer or two (Goldwasser 1987) and possibly do so every night. Such a long distance pollination ability is probably crucial to *Xanthosoma sp.,* as a light-demanding gap species.

The ratio of *C. nigerrima* to *C. sexpunctata* that was found in this study (62%) seems like a reverse in gradual decline of *C. nigerrima* when considering past studies. Craig (2001) recorded a ratio of 2% last April/May which took place at a site about one kilometer away. Also in the Monteverde region, Sica found 13% *C. nigerrima* in April/May of 1999 and Goldwasser found 95% in a study for his doctoral dissertation prior to 1987. These changes are probably related to yearly and seasonal climatic cycles as well as "random" population fluctuations. Insect populations in the tropics are known to be less than stable, commonly fluctuating in response to population concentrations, host density, climatic patterns and especially rainfall (Denlinger 1980). Although these results show a much higher ratio of *C. nigerrima* than in the last few years it must be noted that this study took place on the tail end of the wet season, while Craig and Sica's studies took place at the end of the dry season. Thus my ratio is probably higher than the current year-round average and Craig's is probably lower. Still, my ratio (which may be at a year-round peak considering it s timing at the end of wet season) is much lower than Goldwasser's ratio in the mid-80's. Since neither species has any clear advantages in response to climatic factors while they are in their adult stage, and *C. nigerrima even* seems to adjust to warmer conditions better in their ability to find the food-and-shelter-providing *Xanthosoma sp.* inflorescences, it seems reasonable to suggest that the difference between the two species in climatic specialization may be primarily observed in the larval stage. More must be known about the lifecycles of the scarab species for a comprehensive understanding of the mutualism.

Beetle visitation in *X. undipes* is combination of a plants presentation of visual and olfactory cues, the scarabs' abilities to perceive them, as well as environmental factors affecting the scarab's behavior. Plants may have limited control over visitation rates of beetles by modifying characteristics of their inflorescences that increase olfactory or visual attractions. Characteristics such as size of spathe opening, and the angle a spathe is bent at might be modified by the plant in response to weather cues that could predict beetle activity. However, beetle behavior can be affected by factors such as overstory tree cover of active inflorescences and weather, seeming to be the most important determinant of visitation rate.

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Appendix A.

"The Spathe/Spadix"