Site fidelity in two species of *Cyclocephala* (Scarabaeidae) to *Xanthosoma robumstum* (Araceae)

Margaret Hendricks

Department of Ecology and Evolutionary Biology, University of Colorado, Boulder

ABSTRACT

Mark and recaptured methods were utilized to determine the site fidelity of two species of scarabid pollinators to a patch of *Xanthosoma robustum* in Monterverde, Costa Rica. Sex ratios remained constant with previous studies, exhibiting a higher proportion of males found per inflorescence than females. One-way ANOVA tests of variance supported evidence that female *Cyclocephala* are more prevalent in first day inflorescences. One-way ANOVA tests also concluded that scarab pollinators exhibit no fidelity to the study patch, The existence of a more resource rich patch in the area could account for the low fidelity observed. The selection for low fidelity through differential spadix heating in *Xanthosom*a may be utilized to promote genetic variance within the patch.

RESUMEN

Métodos de marcaje y recapture fueron utilizados para determinar la fidelidad por un stio en dos especies de escarabajos de la familia Scarabidae polinizadores de un parche de *Xanthosoma robustum* en Monteverde, Costa Rica. La proporción de sexos permanece constante con previos estudios, exhibiendo una proporción mayor de machos que hembras encontrados por inflorescencia. Una prueba ANOVA de una vía soporta la evidencia de que las hembras de *Cyclocephala* son más prevalentes en las inflorescencias de un día. La misma prueba también concluye que los escarabajos no exhiben fidelidad por los parches. La existencia de más parches en el área pueden ser los factores influyentes en la baja fidelidad observada. La selección de baja fidelidad a través de las inflorescencias de *Xanthosoma* deben ser utilizados para promover variación genética dentro del parche.

INTRODUCTION

Basic models for habitat selection presume that individual settlement decisions are the result of the thorough investigation and evaluation of all available habitats. Traditionally, the habitat selected reflects the site with optimal qualities (Switzer 1993). Site fidelity can be defined as the extent of which an individual or species is confined to a certain community or location (Buse 1988). The site for which an individual remains faithful could be a territory, breeding ground, nesting site or foraging area (Lanyon and Thompson 1986). Moreover, site fidelity can be determined by characteristics such as reproductive potential (Burger 1982), population pressure (Weatherhead and Boak 1986) and habitat stability, or can be the result of individual life history traits, such as age, or previous reproductive success (Switzer 1993).

Typically, sites that demonstrate predictability or stability of resources often experience high rates of fidelity (Switzer 1993). Site fidelity of insect pollinators to

habitats is often determined by previous assessments of viable habitats within an area (Lanyon 1986). Site-faithful adults seem to receive substantial fitness advantages for familiarity to local condition (Gavin and Bollinger 1988). Insect fidelity is commonly correlated with previous reproductive success. Although it can be said that plants within a given territory for which insect fidelity exists benefit from a constant stream of pollinators, in some cases fidelity can be selected against. For plants that exist in clumps or patches, a decrease in site fidelity serves by pollinators could promote optimal genetic out crossing for the plant and ultimately maximize both individual and patch fitness.

In the case of insect pollinators who maintain mutualistic relationships with their specific host plants, fidelity is traditionally promoted by the plant and then maintained by the insect pollinator. Therefore, mutualisms between an insect pollinator an a plant could be useful in studying site fidelity by a pollinator. From the perspective of a pollinator, if the resource the plant produces is beneficial, the pollinator should exhibit site fidelity. From the perspective of the plant, site fidelity may lead to gentic inbreeding, and there a plant may dissuade fidelity by some physiological machanism.

For this strudy, I used the Cyclocephala-Xanthosoma system to examine site fidelity from the perspective of the insect pollinator. Xanthosoma is an Areceae that has a mutualism involving scarab beetle pollinators. Many aroids exhibit a unique mutualism involving scarab beetle pollination; scarab beetle pollination is a fundamentally different strategy than traditional rapid pollination by foraging animals (Young 1998). In the case of the aroid *Xanthosoma robustum* and its beetle pollinators, it seems probable that fidelity of *Cyclocephala* pollinators should be correlated to inflorescence abundance. Previous studies conducted on the *Xanthosoma:Cyclocephala* pollination syndrome have shown little movement of *Cyclocephala* between near inflorescences; forgoing eligible neighbors for distant inflorescences. (Goldwasser 1987) Although the pollination syndrome has been intensely studied, little is known about the fidelity of *Cyclocephala* to *Xanthosoma robustum*. The study conducted serves to determine the site faithfulness of two *Cyclocephala* species to the Pacific Slope patch of *Xanthosoma robustum*. Since no other known patches of *Xanthosoma* exist in Monteverde, it can predicted that there will be an increase in beetle populations on the Pacific Slope due to immigrations by beetles that previously visited the Atlantic Slope patch. As a result, predictions can also be made that the estimated population sizes for individual species should be double that of those estimated in the spring of 2009. Increases in population size due to an influx of displaced individuals should result in high fidelity of scarab pollinators to the Pacific Slope patch of *Xathosoma robustum*.

MATERIALS AND METHODS

Study Site

This study was conducted over the period of October 27th to November 16th 2009 in Monteverde, Costa Rica. Data was collected from a patch of *Xanthosoma* located on Fred Morrison's property, about .25 of a kilometer down the road from the Monteverde Cloud Forest Reserve. Historically two main patches of *Xanthosoma* have been known in the Monteverde area, one patch on the Atlantic Slope and one patch on the Pacific Slope. In June 2009, the Atlantic Slope patch of *Xanthosoma robustum* was elimated.

Natural History of the Cyclocephala-Xanthosoma System

The pollination of the aroid *Xanthosoma robustum* is the result of the mutualistic partnership with scarbid beetles of the genus *Cyclocephala* (Goldwasser 1987). Two species of Cyclocephala have been found to pollinate local populations of *Xanthosoma robustum* in Monetverde, Cyclocephala *nigerrima* and *Cyclocephala sexpunctata* (Goldwasser 1987). Both species of beetles can be portrayed as sexually dimorphic; males can be distinguished by enlarged tarsi on their forelegs, with females characterized by grooves on elytral edges. *Cyclocephala sexpunctata* are categorized by yellow-brown elytra with brown spots and are typically range in size from 1.0 to 2.5 cm. *Cyclocephala nigerrima* can be differentiated by black elytra and are marginally larger ranging in size from 1.0 to 3.0 cm (Goldwasser 1987). Both *Cyclocephala* species utilize *Xanthosoma* as a resource for mating as well as for a food source.

     Xanthosoma robustum is a tall herbaceous plant with characteristic sizeable "elephant like" leaves and showy white inflorescences (Goldwasser 2000). Flowering of *Xanthosoma robustum* predominantly occurs during the rainy season; each plant produces inflorescences every nine days with up to 5-15 inflorescences per season (Goldwasser 2000). As a result, the flowering phenology of Xanthosoma is such that beetles cannot move between inflorescences on the same plant (Young 1998). Inflorescences are protogynous (Young 1986) and agamous; male flowers are located on the top of the spadix and are separated from the basally located female flowers by a ring of sterile flowers. (Venkatesan 2001). *Xanthosoma* employs the arecous pollination strategy of spadix heating (Gibernau 1999). Thermogenetic respiration, or the release of heat through the conversion of metabolized carbohydrates, serves as the main attractant for beetle pollinators (Craig 2001). On the first night of opening the spadix heats rapidly to 40-42 C and emits a pleasant smelling odor to attract *Cyclocephala* pollinators. The beetles crawl into the chamber containing the female flowers where they mate and feed on the sterile flowers for a period of 24 hours (Ghose 2009). On the second night the spadix heats again to release the male pollen; scarab visitors then crawl up the spadix, inadvertently collecting pollen, which is then carried to newly, opened inflorescences (Goldwasser 2000). Therefore, the pollination syndrome of *Xanthosoma* operates on a 48 cycle.

Data Collection

Data collection was conducted every morning, for eleven days. Each day new inflorescences were located and noted within the patch. Beetles found within each inflorescence were counted, sexed and species were determined. Mark and recapture methods involved the elytral marking of individuals by paint pens. Inflorescences were then marked with corresponding paint pen colors on flagging tape. As well as tagging newly emergent inflorescences, second day inflorescences previously flagged were checked for recaptures or the presence of newly immigrated individuals. When recaptures were discovered, a measuring tape was utilized to determine average flight distance from the original inflorescence.

Statistical Analysis

Mark and recapture techniques allowed for the calculation of population estimates through the Schnabel Method; population size was determined for both Cyclocephala sexpunctata and Cyclocephala nigerrima. The difference in occurrence of females on day 1 versus day 2 was determined through the use of a one-way ANOVA test for variance. One-way ANOVA tests were also utilized to determine fidelity of each species to second day inflorescences.

RESULTS

Results for sex ratios for total beetles recorded within an inflorescence showed 138:19 males to females; sex ratios for recaptures showed 4:1 males to females (Figure 1). The percentage of marked males was 87.9 % (n= 138); the percentage of females marked was 12.1% (n=19). The total number of recaptures was 17 individuals; males accounted for 82.4% (n=14) and females accounted for 17.6% (n=3). There were a greater number of females in first day inflorescences than in second day inflorescences ($F_{1, 36}$ = 5.1892, p=0.0288; Figure 2). A second one-way ANOVA was utilized to determine the fidelity of separate sexes in *Cyclocephala nigerrima* and *Cyclopcephala sexpunctata* to the patch of *Xanthosoma robustum*. Neither species nor sexes showed fidelity to the *Xanthosoma* patch ($F_{1\ 40}$ = 1.848, P= 0.3623; Figure 3) The Schnabel method was utilized to calculate population estimates for both species of *Cyclocephala*. 676 individuals were calculated for the population of *C. nigerrima* and 192 individuals for *C. sexpunctata* (Figure 4).
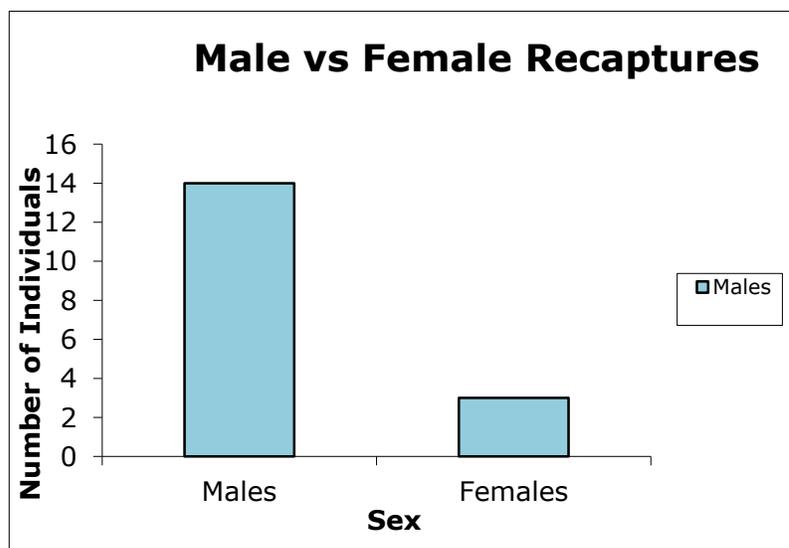

FIGURE 1. Recapture rates show a higher proportion of males to females. Male recapture rates account for 82.4 % (n= 14) and female recapture rates account for 17.6 % (n=3)
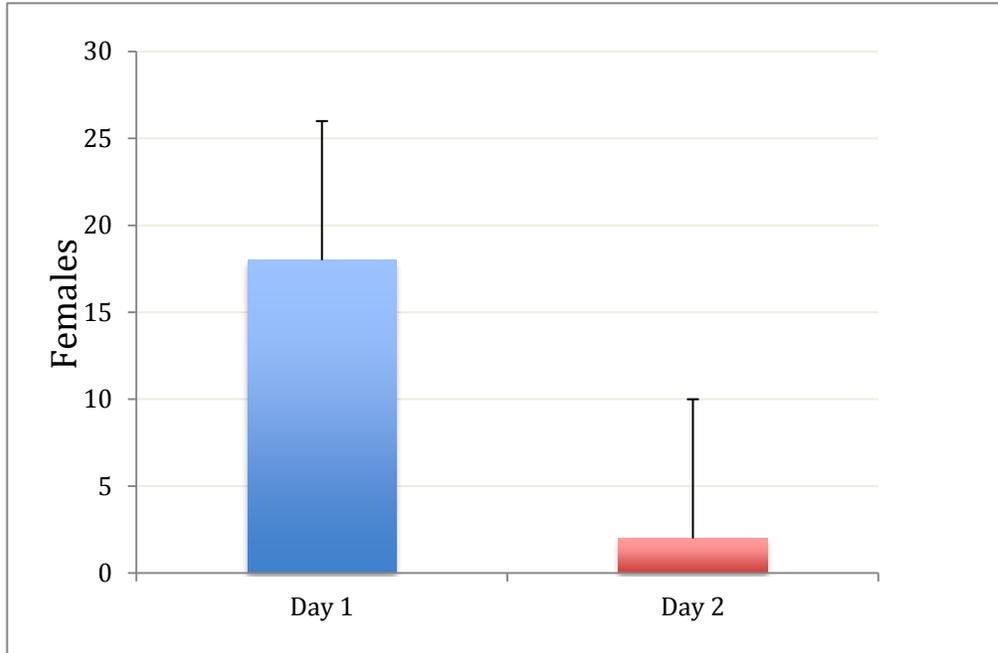
FIGURE 2. A one-way ANOVA shows statistically significant evidence for a higher occurrence of females in Day 1 inflorescences compared to Day 2
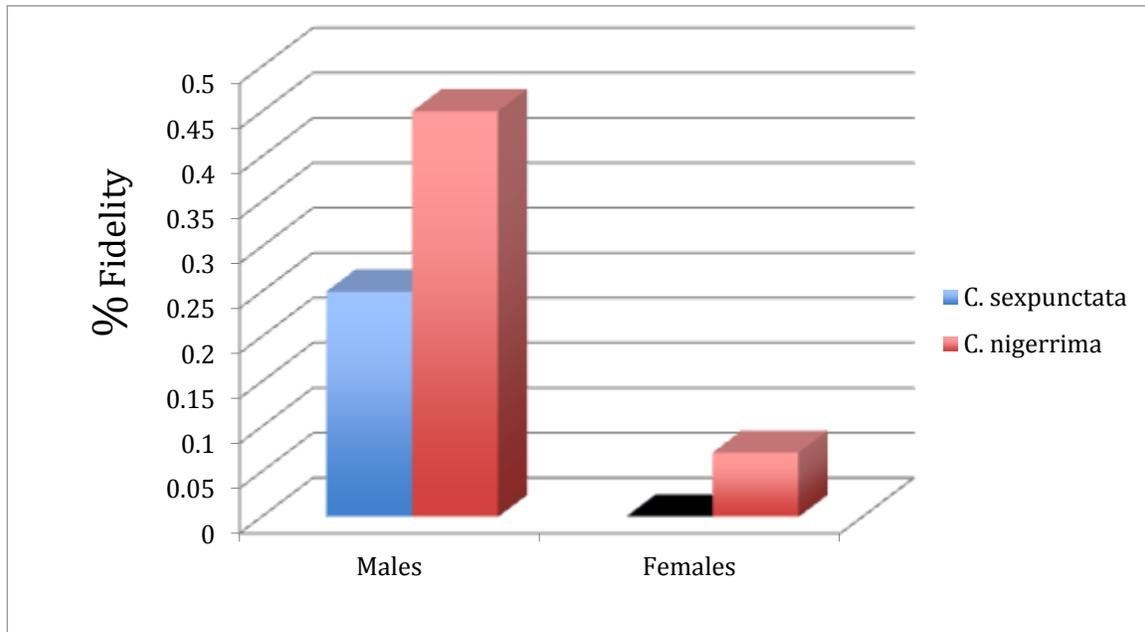

FIGURE 3. The one-way ANOVA for % Fidelity of male and female *Cyclocephala sexpuntcta* and *Cyclocephala nigerrima* to *Xanthosoma robustum* is not statistically significant. No site fidelity is experienced for each species or sex.
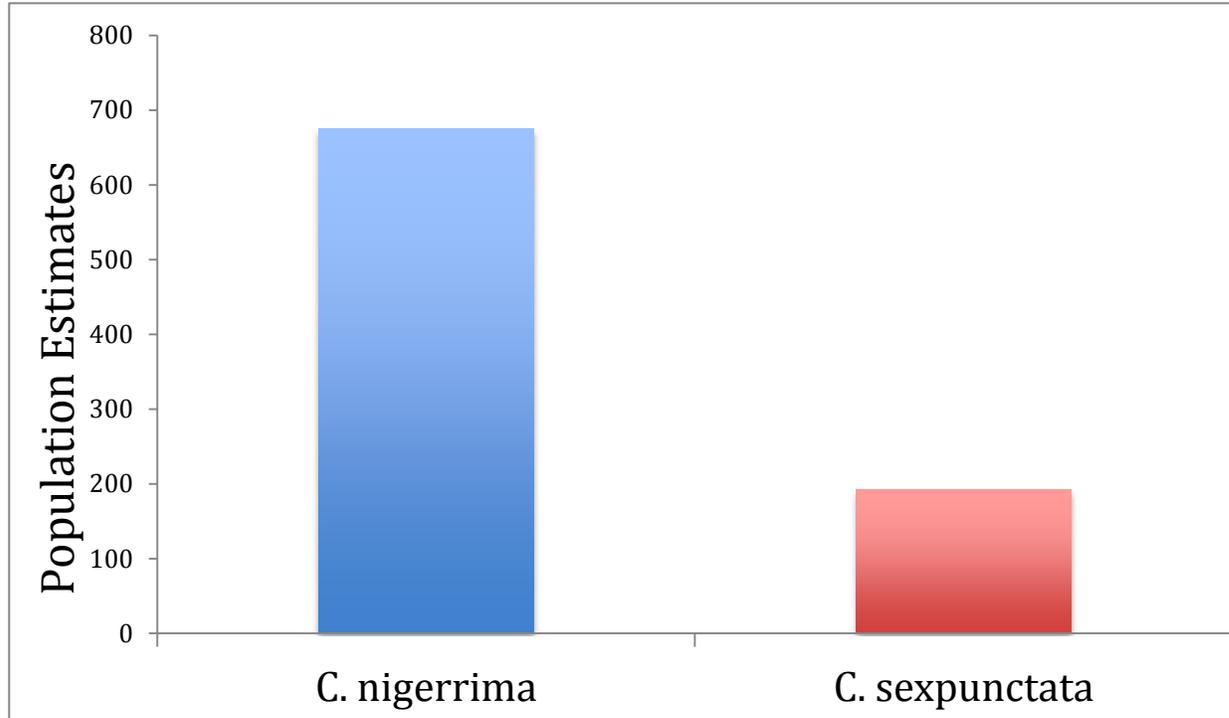
FIGURE 4. The Schanbel method was utilized to determined population sizes. 676 individuals for *C. nigerrima* and 192 individuals for *C. sexpunctata.*

DISCUSSION

Sex ratios obtained correspond with previous studies that observed a strong bias for males in the population; traditionally a 1:3 female to male ratio was detected. Usually, it has been observed that female scarab beetles spend a reduced amount of time within individual inflorescences than that of their male counterparts; typically females visit *Xanthosoma* inflorescences for 40% as long as males (Goldwasser 1987). Although it is known that females visit inflorescences for a shorter period of time, it still remains unknown how females allocate their time outside of inflorescences. A higher ratio of males in the pollinator population serves to account for the differences between relative numbers in the population; therefore it can be determined that no biased sex ratio is implemented at birth (Goldwaser 1987).

There was low site fidelity by both beetle species to *X. robustum*. It is possible low fidelity was found for two different reasons: (1) the existence of another patch in the area, or (2) the selection for low site fidelity of beetles by *Xanthosoma* itself. Traditionally, individuals that experience high reproductive success, like beetles, show elevated probabilities for site faithfulness in the next breeding season (Hoover 2003). Due to the fact that the Pacific Slope patch of *X. robustum* exists as a predictable and stable resource, it would seem logical for scarab beetle pollinators to exhibit high fidelity; however, low levels of site fidelity are found with Cyclocephala. The existence of

another patch of *X. robustum* that contains more inflorescences and therefore more mating opportunities, may account for the lack of beetle fidelity.

It has been found that site fidelity is positively correlated with the cost of changing territories; in other words, organisms will stay in one place if the cost of finding a new site is high. The higher turnover rates experienced by short-lived species serves to diminish movement costs that could potentially discourage the movement of individuals to new habitat; therefore short-lived species are more prone to migrating to better quality habitats. For habitats that exhibit predictability of resources, the movement of current residents out of the existing territory should only occur in the event that a higher quality option becomes available (Switzer 1993). Taking into account the influence of movement costs, turnover rates, and the predictability of resources inflicted on the individual when changing habitats, the alternative patch must be more resource rich than the existing patch in Monteverde. The benefits derived from the other resource rich patch much outweigh the movement costs inflicted on *Cyclocephala*. Seasonality may also account for low fidelity.

One mechanism that may explain the difference in resources among patches is the seasonality in phenology of *Xanthosoma*. *Xanthosoma robustum* has been recored as having a peak in flowering during the wet season on the Pacific slope in Monterverde, Costa Rica. It is possible that, in another location, there where more flowers that the patch I studied. Since the Atlantic slope of Costa Rica has constant abiotic inputs in the form of rain and mist and, therefore, shows less seasonality than the Pacific slope, it is possible that there is a higher abundance of flowers on the Atlantic slope below Monteverde, and *Cyclocephala* beetles show high fidelity of patches on the Atlantic slope. Furthur work on this system should focus on comparisons of Atlantic and Pacific slope phenology and fidelity.

Due to the low fidelity observed by beetle pollinators, it can be concluded that *X. robustum* pheneology successfully operates to deter beetle fidelity. Mark and recapture studies showed exceptionally low recapture rates; confirming long distance pollen flow (Goldwasser 1987). *Xanthosoma* may effectively control *Cyclocephala* fidelity through thermogenetic respiration; due to the fact *X. robustum* plants utilize differential heating times between day one and day two inflorescences and between plants, they successfully control pollen flow via beetle pollinators, as pollinators cannot predict at what time an inflorescence will be receptive (Goldwosser 1987). Due to the fact that *Xanthosoma* exists in a clumped formation, there is an increased likelihood that the patch will experience genetic bottlenecking through restricted gene flow. However the variability in inflorescence heating functions operate to promote long distance flights of pollinators, insuring the optimal outcrossing of genes.

During the rainy season the scarab population experiences high rates of turnover, mark and recapture trials show direct evidence for continuous recruitment in local beetle populations. Continuous recruitment of *Cyclocephala* may be the result of increased immigrations from beetles previously inhabiting the Atlantic Slope patch. Although there is a constant influx of beetles into the population, no exponential increase in population size was noted. Therefore, there must be unremitting departure of existing scarab beetles from the population, ultimately leading to low fidelity (Goldwasser 1987). The departures

from the patch contribute to the notion that a more resource rich habitat exists in the Monteverde region. The assumptions of the Schnabel Method of population estimation presume that there is random mixing within the population (Krebs 1989). It seems probable that scarab pollinators move in a nonrandom pattern through the Monteverde patch of Xanthosoma; as a result the population numbers obtain by the Schnabel Method could be overestimated. Based on recapture rates, it seems probable that both species of *Cyclocephala* move in a unidirectional pattern through the patch. However, my estimate of 614 individuals in the total population supports my prediction that population numbers would more than double (from 200 in Spring 2009) due to the absence of the Atlantic Slope patch of Xanthosoma.

Little remains known about the influence of differential spadix heating and its selection for low fidelity in beetle pollinators, further studies should be conducted to determine if thermogenetic heating by *Xanthosoma robustum* results in increased genetic variance.

LITERATURE CITED

BURGER, J. 1982. The role of reproductive success in colony-site selection and abandonment in black skimmers (*Rynchops niger*). Auk 99 : 109- 115.

BUSE, A.1988. Habitat selection and group of beetles (Coleoptera). Holarctic Ecology 11 : 241-247.

CRAIG, J. 2001. Determinants of morphological characteristics: thermogenetic heating and Scarabaeidae pollination *in Xanthosoma robustum* (Areceae). Tropical Ecology and Conservation Spring 2001 : 30-40.

GHOSE, S. 2009. The effects of *Xanthosoma spp.* (Areceae) temperature,scent, and flowers on the mating frequency of *Cyclocephala sexpunctata* (Scarabaeidae). Tropical Ecology and Conservation Spring 2009 : 9-18.

GIBERNAU et al. 1999. Beetle pollination of philodendron solimoesense (Areceae) in French Guiana. International Journal of Plant Sciences 160 : 1135-1143.

GOLDWASSER, L. 1987. Mutualism and its ecological and evolutionary consequences. PhD Dissertation. University of California, Berkley, CA. Pp. 243-324.

GOLDWASSER, L. 2000. Scarab beetles, elephant ear (*Xanthosoma robustum*) and their associates. Monteverde: Ecology and Conservation of a Tropical Cloud Forest : 268-271.

HOOVER, J. 2003. Decision rules for site fidelity in a migratory bird, the prothronotary warbler. Ecology 84 : 416-430.

KREBS, C. 1989. Schnabel Method. In: *Ecological Methodology*. Harper and Row, Publishers, New York, NY. Pp. 30-36.

LANYON , S.M. and Thompson, C. F. 1986. Site fidelity and habitat quality as determinants of settlement pattern in male painted buntings. Condor 88 : 206-210.

SWITZER, Paul. 1993. Site fidelity in predictable and unpredictable habitats. Evolutionary Ecology 7: 533-555.

VENKATASEN, M. 2001. The movement, composition and behavior of scarab beetles and other insects visiting inflorescence of Xanthosoma robustum (Areceae). Tropical Ecology and Conservation :1-11.

WEATHERHEAB, P. J. and Boak, K.A. 1986. Site infidelity in song sparrows. Animal Behavior 34 : 1299-1310.

YOUNG, H. 1986. Beetle pollination of Diffenbachia longispatha (Areceae). American Journal of Botany 73: 931-944.