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# Nocturnal vs. diurnal insect diversity within tropical montane forest canopy

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## ABSTRACT

Tropical forest canopies are unique environments with complex interactions, allowing for high levels of specialization for insects. The purpose of this study was to test whether increased specialization has created differences in species richness and diversity between nocturnal and diurnal canopy insects. To test this, insects were collected from six trees using suspended traps containing three types of bait (carrion, rotten fruit, and specific scents that attract euglossine bees). Diversity and species richness was quantified for diurnal and nocturnal traps of all three baits and for total number of insects collected diurnally and nocturnally. The results showed that on all accounts there was a significant difference in species richness and diversity for diurnal traps ( $H' = 1.000$ ) and nocturnal traps ( $H' = 0.863$ ) ( $P = 0.005$ ). Diurnal traps had a significantly higher overall abundance, species richness, and diversity than nocturnal traps.

## RESUMEN

Los doseles de los bosques tropicales son ambientes únicos con interacciones complejas, que permiten altos niveles de especialización en los insectos. El propósito de este estudio fue determinar si la mayor especialización ha creado diferencias en la riqueza y diversidad en los insectos nocturnos y diurnos del dosel. Para probar esto, los insectos fueron colectados en seis árboles usando trampas suspendidas que contenían tres tipos de cebo (carroño, fruta podrida, y olores que atraen abejas euglosinas). Se cuantificó la diversidad y riqueza de especies en las trampas diurnas y nocturnas con los tres cebos y para las trampas diurnas y nocturnas en total. Los resultados demostraron que en todos los casos había una diferencia significativa entre la riqueza y la diversidad de las trampas diurnas ( $H' = 1.000$ ) y las trampas nocturnas ( $H' = 0.863$ ) ( $P = 0.005$ ). Las trampas diurnas tenían una abundancia, riqueza, y diversidad significativamente más altas que las trampas nocturnas.

## INTRODUCTION

People tend to view rich tropical communities as full of specialized species, tightly packed, with narrow niches. MacArthur and Wilson (1967) explored this concept in the niche compression hypothesis, which states that as more species become packed into a community, the habitat occupied by each species shrinks. Basset (1996) found 94 different species of herbivorous leaf chewing insects in one tree alone in New Guinea. Insect specialization was found to be high on trees with high species richness and diversity. Similarly, studies done by Marquis and Braker (1994) at La Selva indicate higher specificity of butterflies and acridid grasshoppers in their wet tropical site, allowing for more diversity and species richness within a compact community.

It is thought that high diversity comes about through niche specialization or resource partitioning (Romoser and Stoffolano 1998). In this instance, diversity appears to be maintained through competition, allowing different organisms to co-exist within the

same habitat. What is not known is if these organisms are specializing temporally, with some exploiting resources at night and others during the day.

If specialization leads to diversity and higher species richness, then the canopy of a tropical rainforest should be no different. The diversity and abundance of insects in tropical tree crowns appears to be enormous (Romoser et al.1998). A study by J. Longino in 1994 found a diverse ant population within the canopy on Barro Colorado Island, Panama (Romoser et al.1998). Although not much is known about insect populations within tropical forest canopies, initial studies indicate they exhibit a high level of diversity.

This study compared the species richness, diversity, and abundance of nocturnal versus diurnal canopy insects. It was hypothesized that there would be differences in species richness and diversity between insects found at night and those found during the day, with little overlap between the two.

## **MATERIALS AND METHODS**

### **Data Collection**

This study was carried out in the forest sub-canopy of La Estación Biológica de Monteverde, Puntarenas, Costa Rica between July 19<sup>th</sup> and July 29<sup>th</sup>. Following one of the Quebrada Máquina tributaries near the station, six different trees of two species (*Conostegia oeristediana* (Melastomatceae) and *Cinnamomum sp.* (Lauraceae) were used for sampling. All trees were located at similar elevations (1450-1460m) within the lower montane wet forest life zone (Haber 1991), and exhibited similar height and diameter at breast height. Trees were at least 60 meters apart to insure sample independence.

Three baits were used: fruit, carrion, and artificial scents known to attract euglossinae bees. The fruit bait consisted of rotten banana chunks cut to similar size and placed in the center of the traps on a Petri dish fastened to the platform. Eucalyptus scent and a floral scent were placed on filter paper and thumb tacked to the center of the platform. Fresh beef cubes were placed on a Petri dish in the center (Appendix A). The same baits were used throughout the experiment, replacing the scents everyday and replacing the meat and fruit when necessary.

Each tree was rigged with three traps, each trap containing a different bait. The traps were checked at twelve-hour intervals (dusk and dawn). Ten nocturnal and ten diurnal samples were collected. The total number of individuals was recorded for each site, separated by time of collection (nocturnal or diurnal), and by bait type. Collection occurred by lowering the traps, collecting the insects by hand, and placing them in bags according to what tree and trap the insect was found in. Specimens were brought to the station for identification. Species were separated based on morphological features and later identified to family using field guides (Solís 1999, Zumbado 1999, Ugalde 2002, Arnett and Jacques1981), and the station's reference collections of pinned insects.

### **Trap Design**

The traps consisted of a board platform under a hanging screen suspended in a tree. Bug netting was used to make the trap. Two wire rings approximately a foot in diameter were used at the top and bottom of the trap for stability and shape. The bug netting was draped over one ring at the top and secured to the bottom ring. The platforms were

approximately 30 cm by 30 cm and protruded on all sides of the trap with the net is positioned in the middle. Twelve Petri dishes were secured to the middle of the platform to be used as a retainer for the meat and fruit. Thumb tacks were used to fasten the scented filter paper to the platform (Appendix B).

### **Data Analysis**

A Shannon-Weiner index was used to assess diversity and a Jaccard similarity index was used to determine the overlap between nocturnal and diurnal insects. A modified t-test was used to compare the diversity indices between the diurnal and nocturnal insects collected overall, as well as within each bait.

## **RESULTS**

Twenty-seven different morpho-species were found belonging to five different Orders and twenty-two different Families (Appendix B). Dipterans exhibited the highest number of species found (8), while Coleopterans exhibited the most abundance overall (288 individuals). Twenty-four diurnal morpho-species and 21 nocturnal morpho-species were recorded (Fig. 1). Species richness found within the different baits also followed the same pattern of diurnal dominance with meat 15 diurnal species to 9 nocturnal species, fruit 15 species to 14 species, and scents 9 species to 2 species (Fig. 2).

The total number of insects collected was 581; with 397 found diurnally and 184 nocturnally (Fig. 3). The total number of insects found for each bait was as follows: scents 48 (37 diurnal, 11 nocturnal), meat 416 (276 diurnal, 140 nocturnal), and fruit 115 (83 diurnal, 32 nocturnal)(Fig. 4).

Diurnal traps had significantly higher diversity ( $H' = 1.000$ ) than nocturnal traps ( $H' = 0.863$ ) (Modified t-test,  $t = 2.651$ ,  $P < 0.005$ ) (Fig. 5). Diversity was found to be significantly higher in the diurnal traps for meats and scents: diurnal meat trap ( $H' = 0.746$ ) and nocturnal meat trap ( $H' = 0.570$ ) (Modified t-test,  $t = 3.266$ ,  $P < 0.001$ ), diurnal scents trap ( $H' = 0.763$ ) and nocturnal scents trap ( $H' = 0.132$ ) (Modified t-test,  $t = 5.968$ ,  $P < 0.001$ ). Nocturnal insect diversity was significantly greater for fruit traps. Diurnal fruit trap ( $H' = 0.885$ ) and nocturnal fruit trap ( $H' = 1.100$ ) (Modified t-test,  $t = 3.016$ ,  $P < 0.002$ ) (Fig. 6).

There was a moderate level of overlap between species found in diurnal traps and nocturnal traps (Jaccard = 0.59). The overlap between nocturnal and diurnal insects attracted to meat (0.50) and fruit (0.61) was similar to the overall diurnal vs. nocturnal overlap, but little overlap was found for scents (0.22).

## **DISCUSSION**

The results supported the hypothesis that there would be differences in diversity and species richness between insects found at night and those found during the day. Diurnal insects exhibited higher species richness and diversity. Evidence of specialization was not strong, as the Jaccard index showed a fair amount of overlap between overall night and day sampling (0.593) and between day and night for two of the baits (fruit = 0.61 and meat = 0.50). There was not much overlap found on scents (Jaccard = 0.22), which could mean greater temporal specialization for insects attracted to scent.

There are numerous possibilities that explain why more diurnal insect species and individuals were caught: heavier rain fall at night, temperature fluctuation between night and day, foraging strategies of diurnal and nocturnal insects, effectiveness of traps catching and retaining insects, and bias of baits.

Sampling was done during the rainy season. This has one major implication for insects: rain can hinder flight (Huffaker and Gutierrez 1999). The rainfall accumulated at night was much greater (71.3 cm) than that during the day (53.3 cm). As the majority of the insects that came to the traps were flying insects, this could explain why diurnal species richness, diversity, and abundance far exceeded that of nocturnal insects.

Within the tropics the most significant temperature fluctuation is not seasonal, but diurnal to nocturnal. On average there was a 5.5 degree Celsius temperature change from day to night during the testing period from the 19<sup>th</sup> to the 29 of July. The average day temperature was 21.2 degrees Celsius, while the average nocturnal temperature was 15.7 degrees Celsius. This discrepancy could relate to diversity and species richness between diurnal and nocturnal insects because there may be a greater cost to adapt to lower nocturnal temperatures.

At the level of the individual, available heat, as indicated by body temperature, is the most basic weather variable determining growth and activity (Huffaker, et al. 1999). Certain metabolic activities essential for development, feeding, dispersal, reproduction, and survival may be hampered or impeded by the temperature decrease at night, possibly resulting in higher diurnal diversity, species richness, and abundance than nocturnal statistics.

Diurnal insects can become active once heated by the sun, while nocturnal insects must rely on stored energy. Morris (1967) showed that during colder temperatures even development is prolonged and larvae must feed on older foliage for the webworm, *Hypahntria cunea*. This could force a late emergence from the larval stage for some nocturnal insects and explain why they are found in lower numbers.

The cost of a nocturnal lifestyle may also influence diversity and species richness through foraging strategies. The cost of foraging is high in terms of calories used in flying, so the rewards must be higher at night because the cost is greater (Price 1997). Heinrich (1979) illustrated the importance of maintaining body temperature high enough for flying. For example, a bumblebee cannot fly if its muscle temperature drops below 30 degrees Celsius. Also, foraging during cooler temperatures is usually performed by larger insects capable of temperature regulation (Price 1997). This may have implications for nocturnal insects that do not have the benefit of solar radiation. Also, more nocturnal insects may have been too large for the trap opening, excluding them from the samples.

All traps were designed to attract insects to the platform using bait, leading them to fly upwards when leaving, thus trapping themselves. This worked well for the larger insects such as the Lepidoptera and most Diptera but some smaller insects possibly escaped during collection.

The baits used in this experiment could also have shown a bias toward diurnal insects. Rotting fruit, carrion, and scents all produce a smell. Diurnal insects are more likely to hone in on visual cues than nocturnal insects, but they also use olfactory location. Nocturnal insects should be more perceptive to chemical and olfactory cues than visual, and thus be able to find the traps. For these reasons the baits used should not have

excluded nocturnal insects unless nocturnal insects do not respond to rotting banana, carrion, and eucalyptus or floral scents.

The fruit traps, however, did have a higher nocturnal diversity ( $H' = 1.100$ ) than diurnal ( $H' = 0.885$ ). This may suggest that fruit was biased toward nocturnal insects. Within the diversity at night the abundance (32) was more evenly spread out among the 15 different morpho-species when compared to diurnal fruit insects (83), where the majority of abundance within the 14 morpho-species was found in two Families: an ant belonging to Formicidae (11 individuals) and a fly belonging to Tephritidae (34 individuals).

The abundance of Rove Beetles (Staphylinidae) both diurnally and nocturnally, as well as on meat and fruit was interesting. Their sheer number far exceeded any other insect (272 total, diurnal = 182, nocturnal = 97, fruit = 18, and meat = 261) (Fig. 7). Through personal observation, these organisms would swarm the meat, and almost cover the bait devouring it. Their aggressive behavior could have allowed them to amass in such numbers. Hanski (1990) studied certain carrion arthropod assemblages in southern Finland and found that increased larval density of one dominant carrion species reduced survival, size, fecundity, and longevity of emerging adults of other species, indicating that competition has an important influence on population dynamics. This may indicate why the Rove beetle was found in such abundance in the traps.

Rove beetles occur in a variety of habitats: some larger species are found on carrion, others on the ground or under objects, near streams and lakes, under bark, in fungi, on flowers, or in decaying plant matter (Borror and White 1970). With this much versatility in habitat it is not surprising to find them in the canopy. Although they were mainly found during the day, it was interesting to find them at night as well. Two species of Staphylinidae have been known to exhibit parental care: *Platystethus arenarius* and *Bledius spectabilis* (Hinton 1944). The female lays its eggs in a chamber and will vigorously protect them from other arthropods, including staphylinid adults. If this is the case for some of the species in the traps it would explain the decrease in abundance at night as males may have been present during the day, while females only protecting their eggs may have been present at night.

The Chalcididae wasp was found in fruit and scent traps. Usually this insect would not be attracted to any of the bait used as their larvae are parasites of other insects. Adult Chalcids are parasitoids and will lay their eggs on other insects (Borror and White 1970). For this reason the wasp was most likely not attracted to the baits but followed insects into the traps in order to parasitize them.

Further research needs to be done in order to accurately depict the diversity of nocturnal vs. diurnal insects in the canopy. Testing at different times during the year is necessary to see if climate or weather patterns affect diversity and species richness. A lab experiment controlling for temperature could be performed to find if this affected the results for diurnal and nocturnal results from the field. The most beneficial experiments would involve using different baits. For example feces, different scents, and different types of fruit may attract different species of insects. Some insects specialize on certain tree species, so by changing the species of trees used for sampling one could possibly find more or different diversity.

## ACKNOWLEDGMENTS

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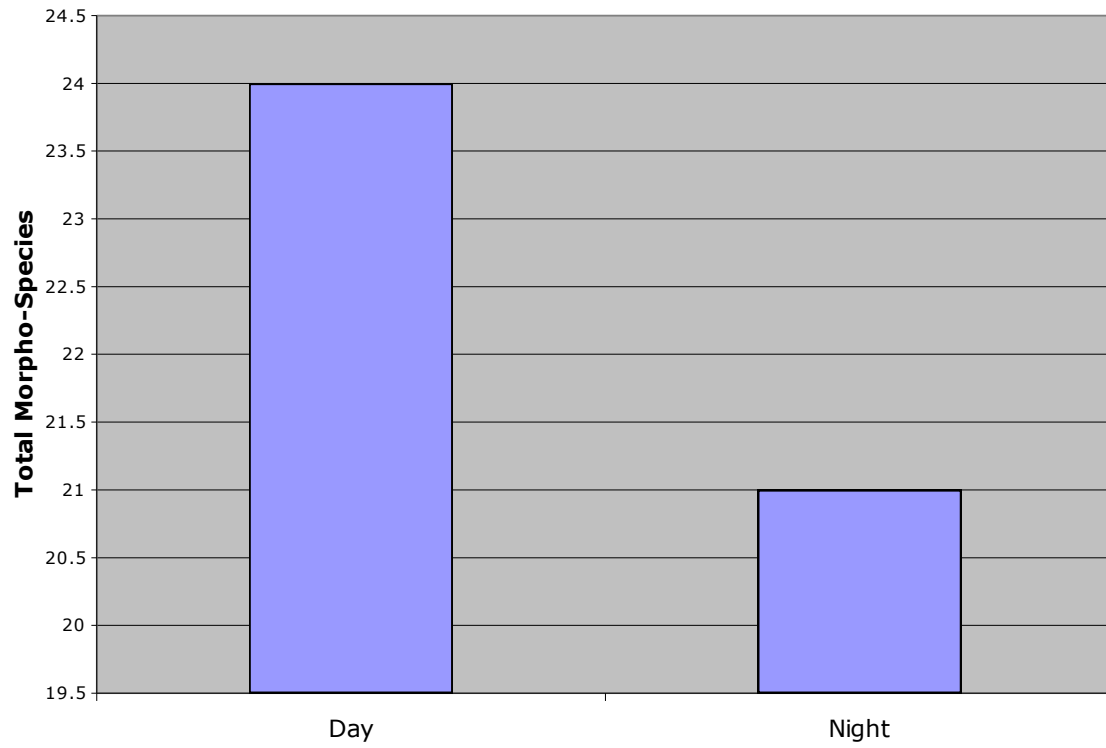
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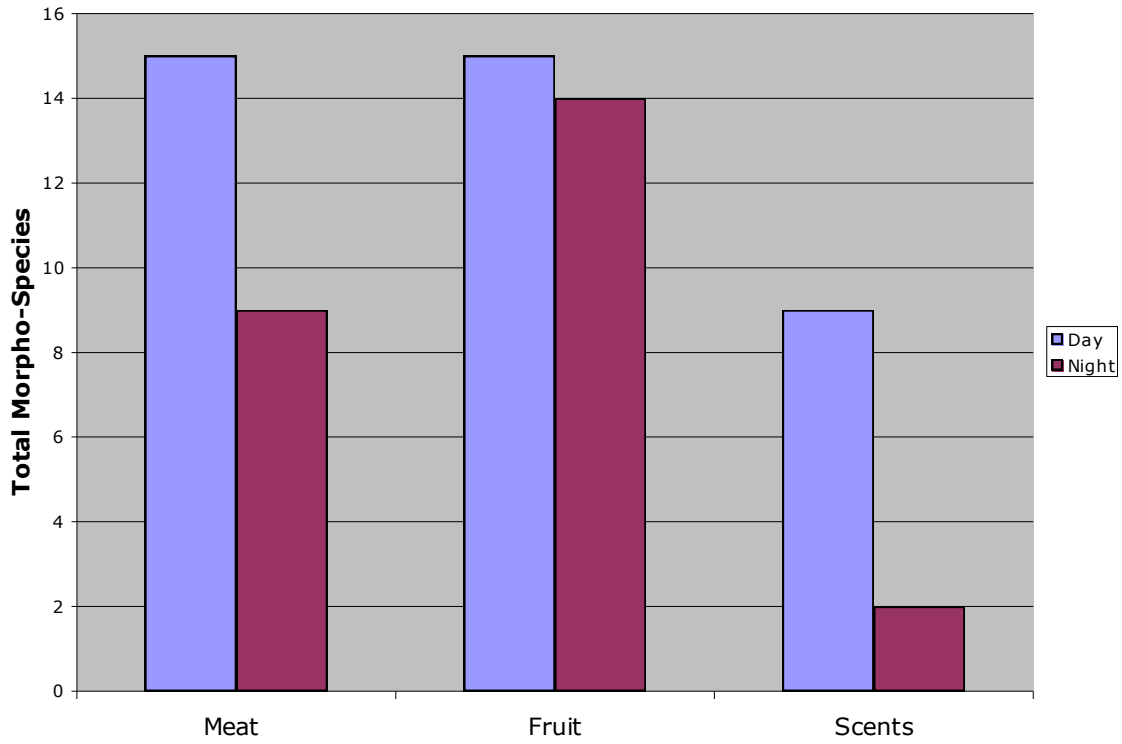




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Figure 1: A comparison of insect species richness attracted to traps suspended in the forest canopy with three baits (carrion, rotting fruit, and scents). Diurnal species richness was higher (24) than nocturnal (21) .

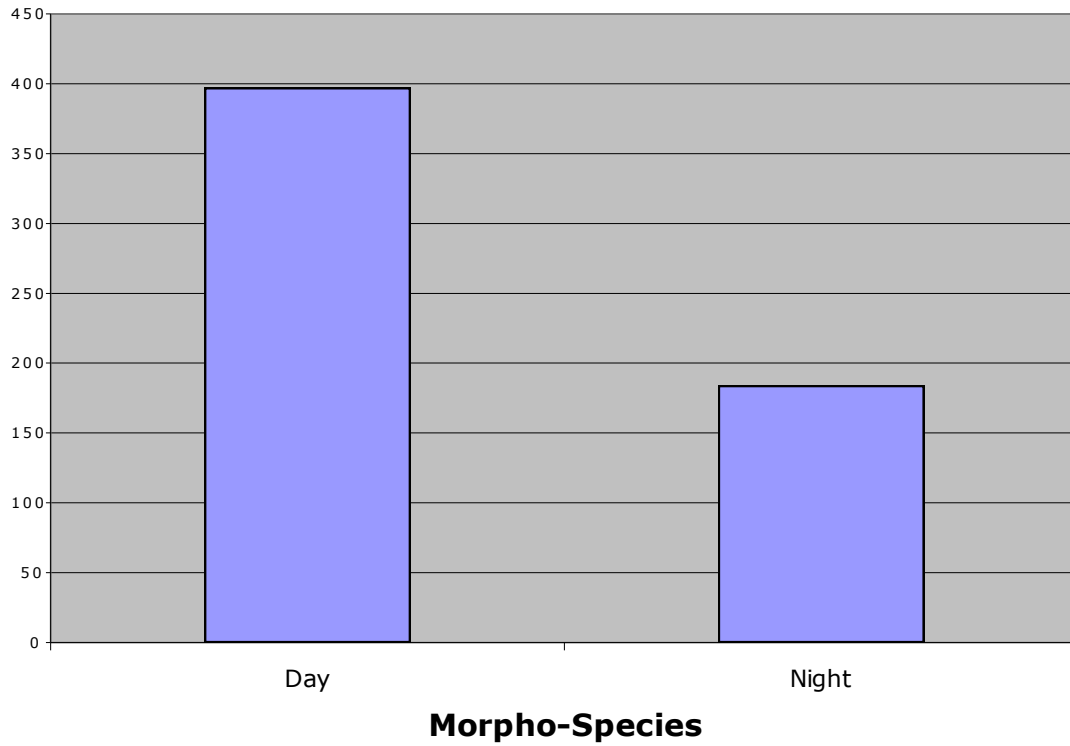
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Figure 2: A comparison of insect species richness attracted to traps suspended in the forest canopy with three baits (carrion, rotting fruit, and scents). This is a break down for all the baits diurnally vs. nocturnally for species richness.

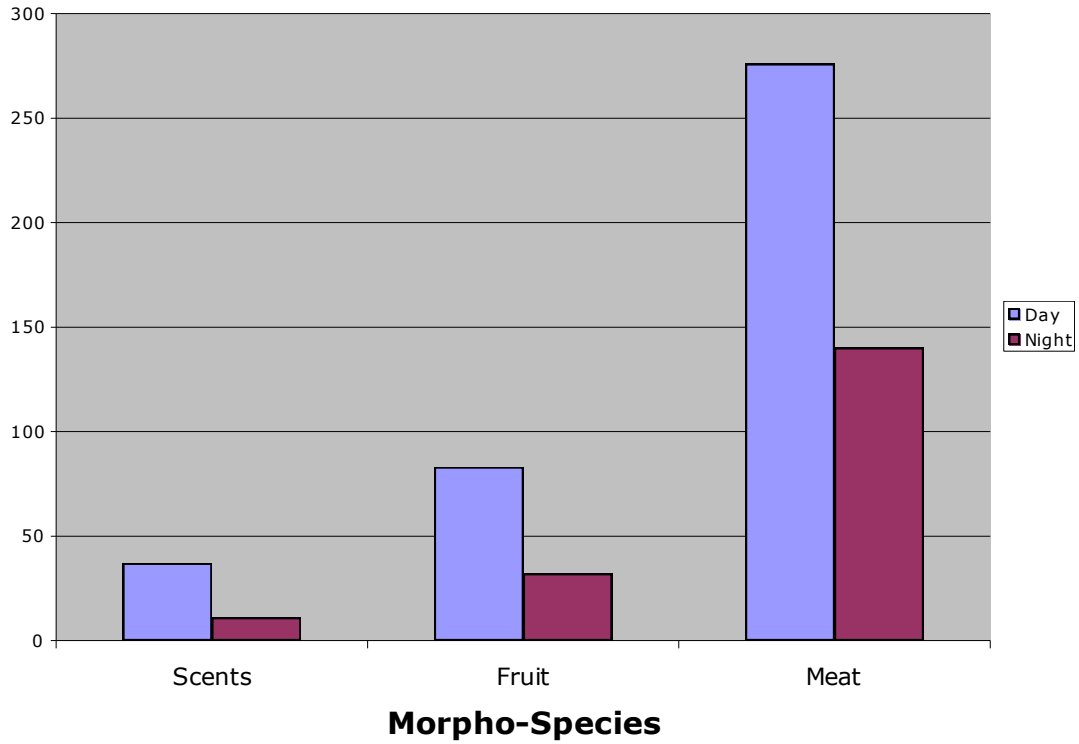
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Figure 3: A comparison of abundance of insect morpho-species found diurnally (397) to nocturnally (184). In all but four instances, diurnal abundance of insects exceeded nocturnal abundance of insects.

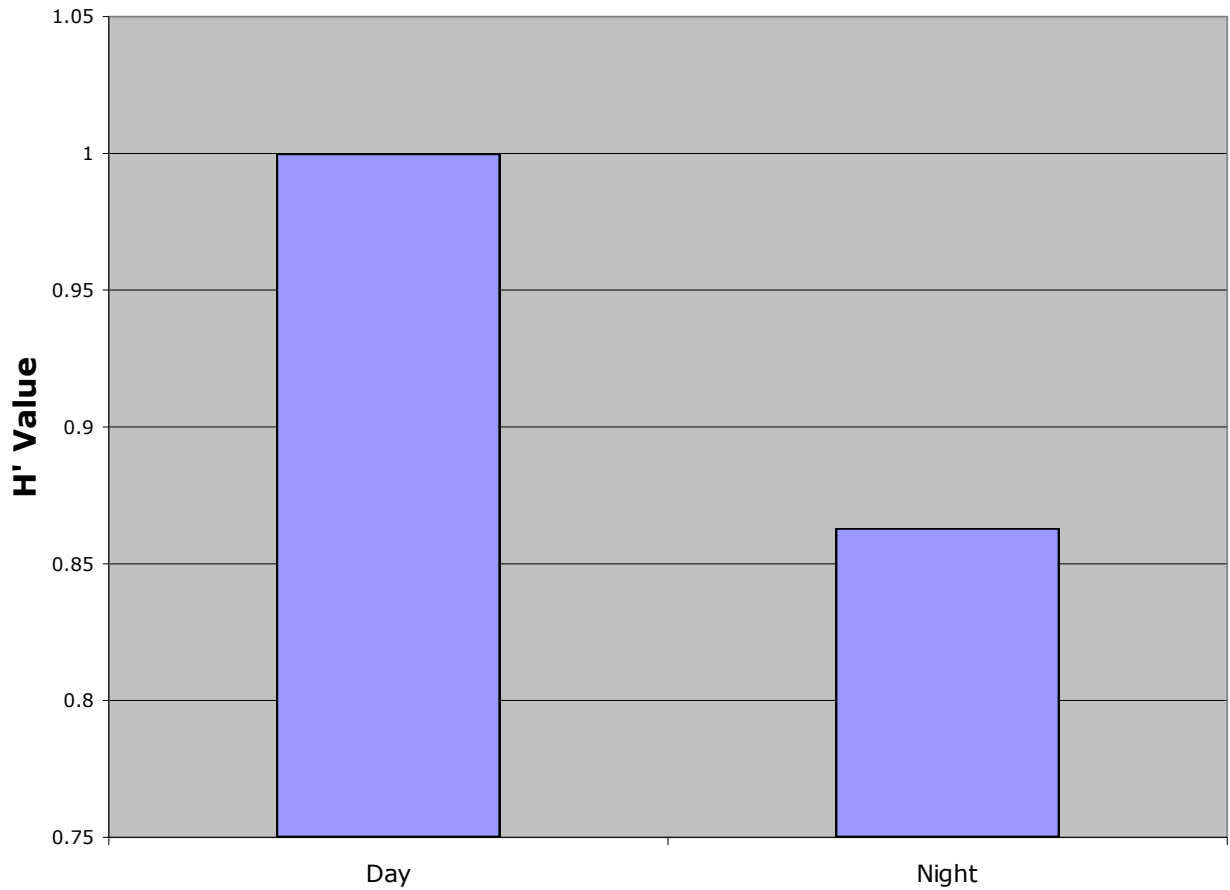
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Figure 4: A comparison of abundance of insect morpho-species found diurnally to nocturnally. The pattern of dominance of diurnal abundance is further emphasized by the break down of each individual trap.

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Figure 5: A comparison of diurnal insect diversity ( $H' = 1.000$ ) and nocturnal insect diversity ( $H' = 0.856$ ). Diurnal insect diversity was significantly greater than nocturnal diversity (Modified t-test,  $t = 2.651$ ,  $P < 0.005$ ).

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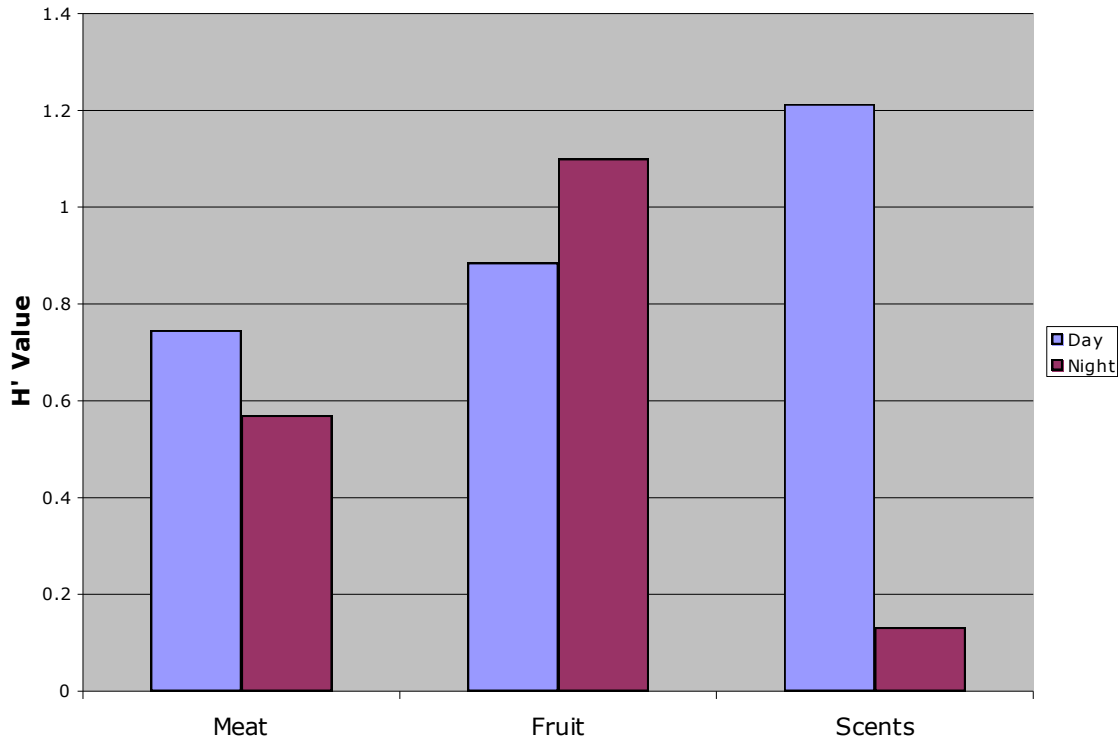


Figure 6: A comparison of nocturnally vs. diurnally insect diversity. Fruit is the only bait where diversity was greater during the night than the day. Diurnal meat trap ( $H' = 0.746$ ) and nocturnal meat trap ( $H' = 0.570$ ) (Modified t-test,  $t = 3.266$ ,  $P < 0.001$ ), diurnal fruit trap ( $H' = 0.885$ ) and nocturnal fruit trap ( $H' = 1.1$ ) (Modified t-test,  $t = 3.016$ ,  $P < 0.002$ ), and diurnal scents trap ( $H' = .763$ ) and nocturnal scents trap ( $H' = 0.132$ ) (Modified t-test,  $t = 5.968$ ,  $P < 0.001$ ).

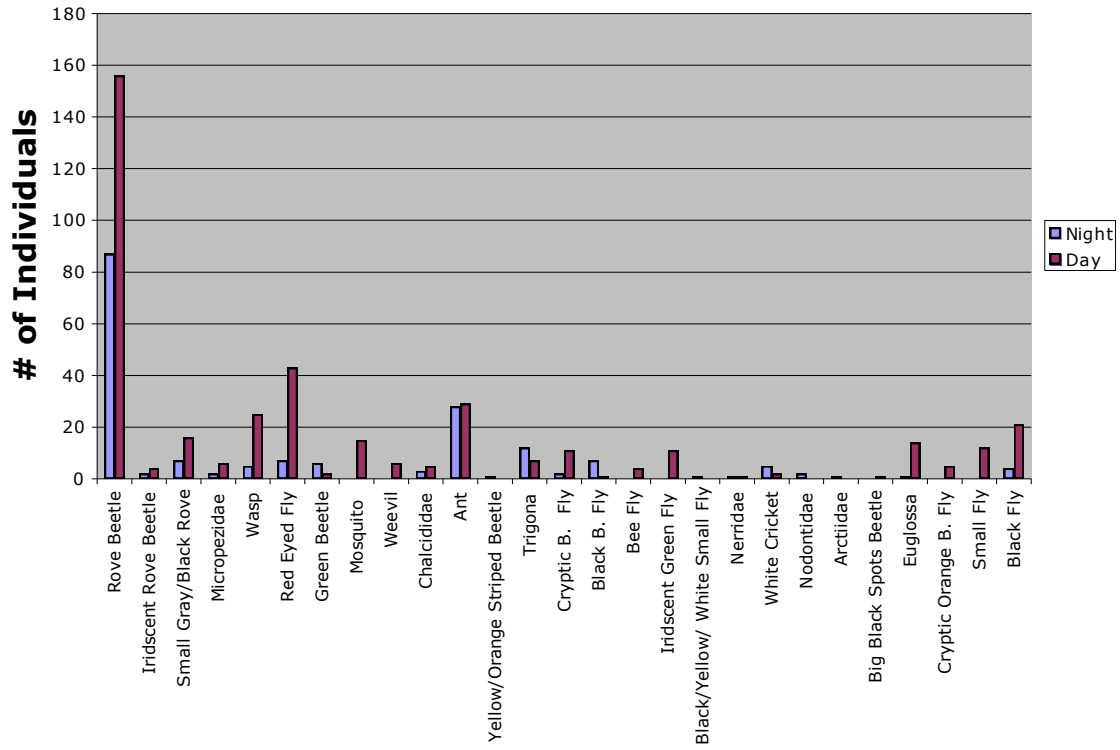


Figure 7: A comparison of abundance of insect morpho-species found diurnally (397) to nocturnally (184). Notice the sheer numbers that the Rove Beetle was found in (262 individuals).

Appendix A: Trap Design

Image only available in physical collection.

Appendix B: There were 27 different morpho-species found in 22 Families, and 5 Orders.  
The genera are only suggested not definitive.

**Morpho-Species**

<b>Order:</b>	<b>Family:</b>	<b>Genus:</b>
<b>Lepidoptera</b>	Nymphalidae	
	Subfamily Satyrinae	Cissia
	Subfamily: Nymphalinae	Smyrna
	Pieridae	?
	Notodontidae	?
	Arctiidae	?
<b>Coleoptera</b>	Silphidae	Nicrophorus
	Chrysomelidae	Chrysochus
	Chrysomelidae	Diabrotica
	Curculionidae	?
	Staphylinidae	?
	Staphylinidae	?
	Staphylinidae	?
	Staphylinidae	?
<b>Diptera</b>	Tephritidae	?
	Sarcophagidae	?
	Syrphidae	?
	Syrphidae	?
	Otitidae	?
	Micropezidae	?
	Neriidae	?
	Culicidae	?
	(fly)	?
<b>Hymenoptera</b>	Apidae	Trigona fulviventris
	Subfamily: Euglossinae	Euglossa
	Vespidae	Agelaia xanthopus
	Chalcididae	?
	Formicidae	Acromyrmex
<b>Orthoptera</b>	Gryllidae	?