May 2011

Fruit presentation and its discovery and removal by frugivorous bats (Phyllostomidae)

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Abstract
Vegetation may obstruct echolocation signals bats use to forage. To compensate, frugivorous bats may use olfaction to locate fruits from a distance, saving echolocation to pinpoint fruits at close range. I observed how discovery time and total fruits taken by bats were impacted by foliage cover. Flight cage experiments found a significantly greater number of ripe fruits taken from feeding stations free of vegetation. Of 511 ripe fruits removed in total, uncovered fruits were taken 70 percent of the time. Also, fruits from uncovered stations were found significantly faster than fruits from covered stations. On average, uncovered fruits were discovered three times faster than covered fruits. Greater removal from feeding stations free of vegetation suggests that olfaction is used to initially find food and that echolocation is compromised and/or vegetation presents a direct, physical barrier that impedes foraging. Surrounding vegetation could compromise seed dispersal of some bat-dispersed plants. Plants should be selected to present fruits away from vegetation.

Resumen

La vegetación puede obstruir las señales de ecolocalización que los murciélagos usan para forrajear. Para compensar, los murciélagos frugívoros pueden utilizar el olfato para localizar frutos a la distancia, dejando a la ecolocalización para ubicar frutos a un rango más cercano. Yo observé como el tiempo de descubrimiento y el total de frutos extraídos por los murciélagos pueden ser afectados por la cobertura del follaje. En experimentos en jaulas de vuelo se encontró, significativamente, un mayor número de frutos maduros extraídos de estaciones de comida libres de vegetación. De un total de 511 frutos maduros removidos, frutos descubiertos fueron recolectados un 70 por ciento del tiempo. También, los frutos de las estaciones descubiertas fueron encontrados significativamente más rápido que los frutos de las estaciones cubiertas. En promedio, frutos descubiertos fueron encontrados tres veces más rápido que frutos cubiertos. Una mayor extracción en las estaciones de comida libres de vegetación, sugieren que el olfato es usado inicialmente para encontrar la comida y que la ecolocalización es comprometida y/o la vegetación presenta una barrera física directa que impide el forrajeo. La vegetación circundante puede comprometer la dispersión de ciertas plantas que son dispersadas por murciélagos. Las plantas deben de ser escogidas para que presenten sus frutos alejados de la vegetación.

Introduction

Frugivorous bats face many difficulties when foraging for fruit. Fruits are often surrounded by branches and leaves, so frugivorous bats must avoid these obstacles while foraging. Foraging phyllostomid bats usually rely on echolocation and acoustical cues to locate food. However, fruits may be acoustically masked by other objects, as when they are nestled in vegetation that obstructs echolocation signals (Korine 2005; Luft 2003). Visual cues are limited as most bats are nocturnal, so bats rely more on olfaction and echolocation (Thies et al. 1998). Odor might be a more reliable cue in a complex habitat because vegetation will not confuse the signal, as is the case with echolocation (Luft 2003). Therefore, from a distance bats can reliably hone in on ripe fruits using smell. Closer, though, echolocation may come into to play as bats eventually must differentiate vegetation from fruit (Thies et al. 1998).

To show that vegetation can impede fruit foraging, I presented ripe and unripe fruits to bats in a flight cage where some fruits are surrounded by vegetation. If olfaction is a primary cue, fruits should be discovered and eaten at the same rate. If echolocation is compromised, unobstructed fruits should be discovered and taken more easily. If the bats are not able to successfully navigate to vegetation-covered fruit, this could compromise seed dispersal of understory plants relying on bats.

Methods

Study site.- My study took place at the Bat Jungle in Monteverde, Costa Rica, which is equipped with a large jungle-simulated flight cage of dimensions 17 m x 2-3 m x 2.5 m, containing 96 free-flying bats, 70 of which are frugivorous. There is only red dim light present in the flight cage and the adjoining viewing hallway, so the bats are not able to use vision to a great extent, but there is sufficient light to observe and record the bats' behaviors.

Study Organisms.- There are five species of frugivorous bats in the Bat Jungle- *Artibeus jamaicensis, Artibeus toltecus, Artibeus lituratus, Platyrrhinus vittatus, Carollia sowelli. A. toltecus* is the most abundant bat at the Bat Jungle with 50 individuals, followed by *C.* sowelli with 8, *A.* jamaicensis with 5, *A. lituratus* with 4 and *P. vittatus* with 3. All phyllostomid bats have leaf noses that can influence the pattern of sound radiation away from the bat (Bogdanowicz 1997). Many frugivorous phyllostomid bats specialize on the fruits of shrubs and understory trees and forage close to ground level (Bonaccorso & Gush 1987). About two-thirds of the bats were born in the wild, and about one-third were born at the Bat Jungle (LaVal 2011). All bats are maintained on a diet of bananas, papaya, melon and watermelon. Species were not differentiated for the experiments. Therefore, fruit discovery and removal could have resulted from any of the species in the enclosure.

Data Collection.- I used the two hanging wooden feeders provided by the Bat Jungle (Fig. 1). These are the feeders normally used to feed bats their maintenance diet. Each feeder has four platforms or feeding stations. The "bananas" in the figure are wood and sit below the feeding platform. Therefore, they do not obstruct food. I used the top-most and second highest feeding stations in the left feeder and the second highest and bottom-most feeding stations on the right feeder as these were at approximately the same height and were easiest to observe. Preliminary trials using the bats' normal fruits and no foliage cover on either feeder showed that there was no preference for either feeder or feeding station.

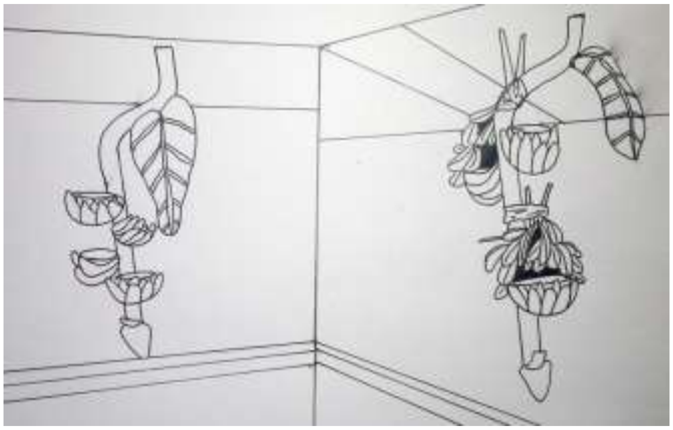

Figure 1.- Experimental setup in the flight cage at the Bat Jungle in Monteverde, Costa Rica. Two bowls of ripe and unripe *Solanum umbellatum* fruits were placed in one hanging banana feeder with *Clusia* sp branch cover (right), while the other feeder would have two bowls of ripe and unripe *S. umbellatum* without *Clusia* sp cover (left). The foraging behaviors of frugivorous phyllostomid bats were observed from this viewpoint.

For two of the feeding stations, I placed fruit on the platform and surrounded it with *Clusia* sp branches. I chose to use *Clusia* sp foliage because it is succulent and long-lasting. I kept the arrangement of the branches open enough so as not to obstruct the fruits' scent and to allow bat movement into and out of the foliage to the fruit, while still covering the shapes of the fruits. Feeding stations had either all ripe or all unripe fruits. One feeding station of each type was surrounded by vegetation while the other was not. Also provided on the feeding stations were the bats' normal fruits.

Each day I would switch which feeder had the foliage. I monitored the four feeding stations over 15 minute trials starting at 8:30 A.M. when the bats were let out of their dormitory room, a room adjacent to the flight cage where the bats sleep at night, into the flight cage for the day. I determined 15 minutes to be the optimal duration because that is when a significantly greater number of ripe uncovered fruits had been taken. Time was started when the door to the dormitory was opened.

I used three different methods for observation of fruit consumption. These methods are only slightly different and were imposed by constraints on accessing feeders to replenish fruits. Despite their differences, they did not compromise later comparisons.

Method 1.- I filled each feeding station with 30 ripe or unripe fruits, then stood in the viewing hallway outside the glass wall of the flight cage and observed the bats finding the fruits. After 15 minutes I removed all the feeding stations and counted how many *S. umbellatum* fruits had been taken from each feeding station. This method of observation was repeated for four days.

Method 2.- I filled each feeding station with 30 ripe or unripe fruits, then stood in the viewing hallway outside the glass wall of the flight cage and observed when the first ripe fruit was found and consumed from both the foliage- covered and uncovered feeding stations. I used three multiple, consecutive 15 minute trials. After the first and second trial ended, I would count how many fruits had been taken from each feeding station and refill the feeding stations so that each one had 30 fruits again. I would restart the time once all the feeding stations had been refilled. At the end of the third trial I would remove all four feeding stations and count how many fruits had been taken. This method of observation was repeated for three days.

Method 3.- I filled each feeding station with 60 ripe or unripe fruits, then stood in the viewing hallway outside the glass wall of the flight cage and observed when the first ripe fruit was found and consumed from each feeding station. I used three multiple, consecutive 15 minute trials, but this time I did not replace fruits at the end of the first and second trials. Instead, I counted each time a bat found and carried away a fruit from one of the feeders. At the end of the third trial I removed the feeding stations from the flight cage. This method of observation was repeated for five days.

Results

Ripeness vs Unripeness.- There was a significantly greater total number of ripe than unripe fruits taken, regardless if they were in uncovered or covered feeding stations. (paired t-test, t= 9.9, df= 23, P= 0.0001). On most days, zero unripe fruits were taken. Since so few unripe fruits were taken, further statistical comparison is not necessary.

Data Collection.- There was a significantly greater number of ripe fruits taken from the feeding station with foliage cover than the feeding station without foliage cover (Sign Test, - = 12, 0=0, +=0, P< 0.05). Of 511 ripe fruits removed in total, uncovered fruits were taken 70 percent of the time.

Method 1.- There were a greater number of ripe *S. umbellatum* fruits taken from the feeding station without foliage cover than the feeding station with foliage cover and this difference was significant (chi-squared goodness-of-fit test, χ^2=34.4, df= 1, P< 0.05; Fig 2.A). The uncovered feeding station had 2.7 times more total fruit taken than the covered feeding station. The feeding station without foliage cover had a mean of 29.75 fruits taken (sd ± 0.5, n=119), while the feeding station with foliage cover had a mean of 11 fruits taken (sd ± 2.94, n= 44).

Method 2.- There was a greater number of ripe *S. umbellatum* fruits taken from the feeding station without foliage cover than the feeding station with foliage cover for the first 15 minute trial and this difference was significant (chi-squared goodness-of-fit test, χ^2= 6, df= 1, P< 0.05) (Fig 2.B). The uncovered feeding station had 1.5 times more total fruit taken than the covered feeding station. The feeding station without foliage cover had a mean of 30 fruits taken (sd ± 0, n= 90), while the feeding station with foliage cover had a mean of 20 fruits taken (sd ± 6.24, n= 60).

Method 3.- There was a greater number of ripe *S. umbellatum* fruits taken from the feeding station without foliage cover than the feeding station with foliage cover for the first 15 minute trial and this difference was significant (chi-squared goodness-of-fit test, χ^2= 58.9, df= 1, P< 0.05) (Fig 2.C). The uncovered feeding station had 3.4 times more total fruit taken than the covered feeding station. The feeding station without foliage cover had a mean of 30.6 fruits taken (sd ± 2.79, n= 153), while the feeding station with foliage cover had a mean of nine fruits taken (sd ± 5.61, n= 45).

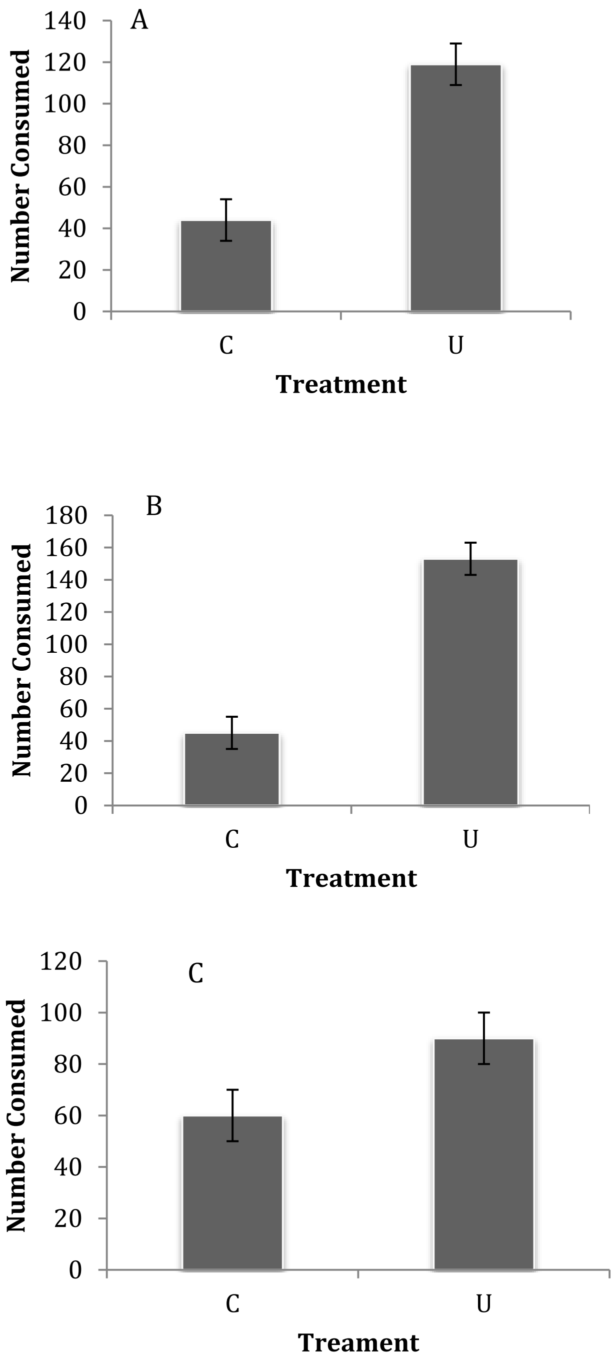

Figure 2. Feeding trials of 15 minutes duration conducted in a flight cage at the Bat Jungle in Monteverde, Costa Rica, showing how many total *Solanum umbellatum* fruits were found and consumed by phyllostomid bats for covered (C) by *Clusia* sp foliage and uncovered (U) feeders over all trial days when (A) used set amount of 30 fruits per day

for 4 days (B) reset number of fruits to 30 for each subsequent trial, for 3 days and (C) used set amount of 60 fruits, for 5 days. Standard error bars given.

Second Trials.- For the second set of 15 minute trials, there was a greater number of ripe fruits taken from the feeding station without foliage cover than the feeding station with foliage cover and this difference was significant (chi-squared goodness-of-fit test, (χ^2= 17.9, df=1, P< 0.05; Fig 3). Uncovered feeding stations had about two times more fruit taken than stations without foliage. The feeding station without foliage had a mean of 16 fruits taken (sd ± 9.68, n= 112), while the covered feeding station with foliage cover had a mean of 8.14 fruits taken (sd ± 5.87, n= 57). The third method had about double the average number of fruits taken from the feeding station without foliage cover compared to the average of the second trial, and about the same average taken from the covered feeding station.

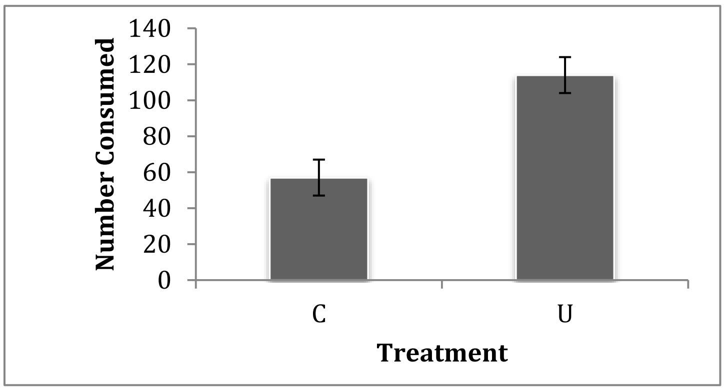

Figure 3. Second set of 15 minute trials conducted in a flight cage at the Bat Jungle in Monteverde, Costa Rica, showing how many total *Solanum umbellatum* fruits were found and consumed by phyllostomid bats for covered by *Clusia* sp foliage (C) and uncovered (U) feeders over 7 trial days. Standard error bars given.

Third Trials.- The same number of total fruits were taken from both the uncovered and covered feeding stations (Fig 4). The uncovered feeding station had a mean of 11 fruits taken (sd ± 11.59, n= 25), while the covered feeding station also had a mean of 11 fruits taken (sd ± 7.83, n= 52). On the same days there were usually more fruits taken from the first and second trials compared to the third trials. Method three had about three times and the second trial had about 1.5 times the average amount of fruits taken from the uncovered feeding station than that for the third trial. This was due to the uncovered fruits running out before the trial was over.

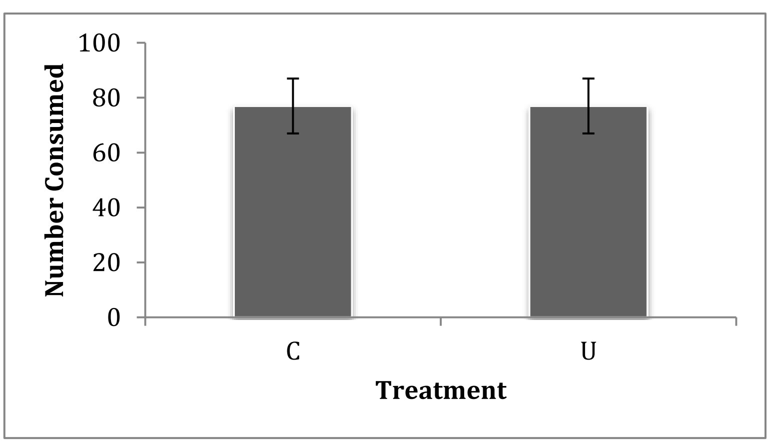

Figure 4. Third set of 15 minute trials conducted in a flight cage at the Bat Jungle in Monteverde, Costa Rica,showing how many total *Solanum umbellatum* fruits were found and consumed by phyllostomid bats for covered by *Clusia* sp foliage (C) and uncovered (U) feeders over

7 trial days. Standard error bars given.

Discovery Time.- The bats discovered the first piece of fruit from the uncovered feeding station significantly faster than the covered feeding station (paired t-test, t= 2.17, df=7, P= 0.04; Fig 5). The average time of discovery for the covered feeding station, 37.6 seconds, was about three times higher than for the uncovered feeding station and on most days the discovery time for uncovered fruits was substantially faster than that for covered fruits.

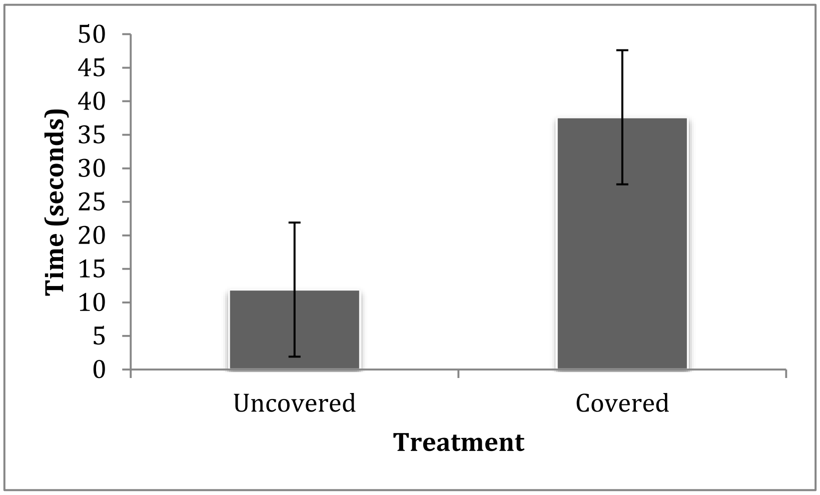

Figure 5. Length of time it took for a phyllostomid bat to find and consume the first *Solanum umbellatum* fruit in a flight cage at the Bat Jungle in Monteverde, Costa Rica. Means and SE given.

Additional Observations

Often times, the bats would fly up to the foliage-covered feeder, hover for a second, and then fly off. This was observed more times for the ripe covered feeder than the unripe. During preliminary trials, the foliage was too dense surrounding the feeding stations and the bats had a harder time entering the feeding stations to get to the fruit. In these cases, I observed that there were more instances of bats approaching, hovering and flying away from the covered feeder. Also, the bats would infrequently knock the foliage into undesirable positions when exiting the feeding station, thus making it harder for the next bat to enter the feeding station.

Discussion

The frugivorous phyllostomid bats at the Bat Jungle had no interest in unripe *S. umbellatum* fruits. They spent very little time investigating these feeders. This suggests that ripe fruits have an odor that is attractive to foraging bats and is used as a cue to find them.

Bats greatly preferred uncovered ripe fruits to the covered ripe fruits regardless of methods, except for later trials where there was no fruit replacement and uncovered ripe fruits ran out. This suggests that bats use olfaction from far away and echolocation up close to detect fruits. For the covered feeders, it is possible that sometimes they were not able to detect the fruits amid the vegetation obstructions using echolocation. This explanation is further supported by my observations that the bats would often hover at the covered feeders (usually the one with the ripe fruits) for a moment and then fly off. This behavior can be explained by the bats smelling the fruits from far away, and failing to try to distinguish vegetation from fruit using echolocation up close. The echolocation signals were probably obstructed by the leaves. The preference for the uncovered feeding station could also be in part due the bats having some difficulties entering the covered feeding station due to undesirable *Clusia* sp branch arrangement. However, they made it into the covered bowls many times, even on days when the foliage placement was not ideal. This could demonstrate that echolocation is an important foraging cue, as the bats would probably not have been able to navigate the foliage obstructions without it. It is also possible that the bats preferred the uncovered to covered feeding station because navigating the foliage obstructions took more energy than taking the fruits from the uncovered feeding station.

Occasional second and third trials without fruit replacement sometimes found no difference between covered and uncovered ripe fruits taken. This was most likely due to all ripe fruits having been consumed. In some cases where only a handful of uncovered ripe fruits remained, bats switched to the ripe covered feeder. This could be an additional sign that olfaction is important, as more ripe fruits in the covered feeders would be expected to give off a stronger odor.

Although the numbers of fruits taken from covered and uncovered feeding stations were significantly different, the overall numbers of fruits taken from the covered feeding station were large enough to show that the bats do not primarily use echolocation to detect and acquire their fruits. If they used primarily echolocation to find fruits at close range, then few or no fruits would have been taken from the foliage-covered feeding station. Thus, they must use olfaction to a certain extent in combination with echolocation.

Covered fruits were discovered much faster than uncovered fruits. This further supports that bats prefer unobstructed fruits to obstructed fruits. This can be explained in part because unobstructed ripe fruits might allow a stronger odor to be given off and be easier to detect. Also, the foliage cover probably made it more difficult to locate the fruits right away, as echolocation signals could have been obstructed.

Therefore, I can conclude that frugivorous phyllostomid bats use smell to locate fruits. Also, they use olfaction from far away and echolocation from up close. Since frugivorous phyllostomid bats prefer unobstructed to obstructed fruits, plants do not have to, but should, present fruits in an unobstructed way. For many, this could mean displaying the fruits on a tall inflorescence or peduncle that would lift the fruits away from the leaves and branches, thus making it easier for bats to discover and remove them and be able to disperse their seeds. Bat-dispersed plants should be selected to present their fruits away from their vegetation to increase dispersal.

Acknowledgements

I would like to thank Richard LaVal, Fabio, Kelly, Vino and Doris for all their help, guidance and patience at the Bat Jungle. It was an honor and a pleasure to be able to conduct research there. I would also like to thank Jim Wolfe and the Centro de Educación Creativa for letting me collect fruits on their properties. Last, thank you Alan Masters for being an understanding advisor, helping me with statistics and driving me around to look for fruits- we succeeded eventually.

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