# Observations of Birds Feeding in Gumbo Limbo and Huevos de Caballo in Costa Rica

Craig Leslie Jackson[1]

[1]none

June 27, 2023

**Abstract**

A study of bird frugivory in Desamparaditos de Puriscal in Costa Rica in 2021 showed the importance of two tropical trees, Gumbo Limbo (Bursera simaruba) and Huevos de Caballo (the common Spanish name of Tabernaemontana donnell-smithii) within habited areas. The study also focused on which species fed on lipid-rich fruits and which fed on lipid-poor fruits — Gumbo Limbo fruits are lipid-poor, whereas Huevos de Caballo "fruits" are lipid-rich — and whether the feeding choices of various birds in this community would reflect the distinction in lipid content. The study was done during the beginning of the rainy season, and compared with a recent analysis of bird frugivory studies. Results showed numerous similarities regarding the birds feeding on Gumbo Limbo, but more differences were found for the birds feeding on Huevos de Caballo. Most significant was that a number of species were observed feeding on both of these fruits that had not been observed in the other studies. Additionally, the study indicated that both trees might be important nutritional sources for young birds. A follow-up study was conducted in 2022. That study showed more feeding by some species on Gumbo Limbo fruits, and demonstrated the importance of Gumbo Limbo for these species during the late dry season. The 2022 study began on 26 January and ended on 7 March, the date when the 2021 study began. Data from 2022 (summarized in Appendices 3 and 3A) will not be fully analyzed, but may be referred to in the discussion.

## 1. INTRODUCTION

Frugivory is an important means of nutritional intake, and is practiced by many birds in the tropics. Since different fruits are available virtually year-round whereas insects may not be, it can often supplement and sometimes become the dominant diet of normally insectivorous as well as normally frugivorous species. It is important for both migrants and resident birds and engaged in by many different families of birds (Snow 1981, Jordano 1987, Albrecht et al. 2018).

A number of frugivory studies have been done previously in Costa Rica ( e.g., Levy 1987, Loiselle and Blake 1990, Wilms and Kappelle 2006, and Thornton et al. 2015). Most had either been undertaken in tropical lowlands and/or on the Caribbean side of the country. They had also been conducted in relatively uninhabited areas. None of them, however, seems to have been conducted in Tropical Moist Forest of Pacific "middle elevations."

A detailed study of birds feeding on *Huevos de Caballo* had also been done by McDiarmid et al. in 1977. This study was done in Tropical Dry Forest at lower elevation in the Costa Rican province of Guanacaste. In this part of the country the vegetation and bird life are also significantly different than the Pacific side of the Central Valley.

Several studies of trees in the family *Burseracae* have also been done. In a study done in Panama (Griscom et al. 2007), Gumbo Limbo was fed on by 21 different species of birds. Two other studies were cited by them (Trainer & Will 1984 , Greenberg et al. 1995) which had shown Gumbo Limbo to be a major food resource in Mexico and Central America. The family of Gumbo Limbo, *Burseracae,* had also been previously cited

as one of the three most important plant families for specialized frugivores (Snow 1981). Another study of birds feeding on a close relative of Gumbo Limbo, *Bursara longipes,* was done in Mexico (Almazan-Nuñez 2016). In this study twenty species of birds fed on its fruits. Observations were made at three different stages of succession of the trees. Species of the family *Tyrannidae* (Flycatchers) were the most frequent visitors in all three stages of succession, and except for the stage of mature succession they also consumed the most fruit.

After having seen a presentation by Tomás Carlo on frugivory in the tropics (2021), several questions had arisen in my mind. Since medium-sized flycatchers had been the most frequent frugivores, I wondered whether size had played a part. Additionally, he had stated that certain bird families preferred fruits high in lipids, while others preferred fruits that were low in lipids. I wondered which types of fruits were being eaten in my town, Desamparaditos de Puriscal, and if I could show a similar preference. I had emailed him for further information and he had sent me a copy of the paper by Pizo et al. (2020) which showed the lipid contents of different plant families.

Since both Gumbo Limbo (low in lipids) and *Huevos de Caballo*(lipid-rich) were both fruiting at the time, I conducted a study of birds visiting and/or feeding on them while I was in Costa Rica in 2021. The study further sought to determine if these trees were also an important food resource for birds on the Pacific side of the Central Valley of Costa Rica, and how they helped to maintain a greater diversity of birds in a more inhabited area of the country.

## 2. METHODS

### 2.1 Study area

Desamparaditos de Puriscal is located in the province of San José, Costa Rica. The town is on the Pacific side of Costa Rica and its elevation is around 850 meters above sea level. It is located north of the main local city, Santiago de Puriscal, which is at least 500 meters higher. The area can best be classified as Tropical Moist Forest (Janzen 1983) with a rainy season that begins in March and continues through September/October. Since prevailing winds during the rainy season are from the south, Desamparaditos finds itself in the rain shadow of Santiago, and its annual rainfall is considerably less. Thus, during the rainy season, on most days a dry morning is followed by a rainy afternoon, and a clear night. Although heavy tropical rains (*aguaceros* ) sometimes continue throughout the day, they are much more likely to only happen in the afternoon, and at the most last several hours.

### 2.2 Study sites

Gumbo Limbo and *Huevos de Caballo* trees both grew in areas where I did my daily bird walks. I therefore decided to incorporate the study into my birding routine, spending time at each one of the trees I encountered. Thus, the times and days when I observed each tree was dependent on which route I took that day, how far that tree was from my house, how long I took on other parts of the walk, and how far it was from the terminus of the walk, which affected whether I revisited it on my return. Given that variability, I tried in some way to normalize my observations by limiting most of them to approximately one half-hour (although at times I did less, and other times more).

During the study, the trees observed probably ranged in elevation no more than 100 meters either above or below the town's elevation (850 meters above sea level), and usually much less than that. All but one site were adjacent to or very close to major roads. The study was conducted over more than two months, with the first observations on 6 March 2021, and the last observations on 12 May 2021. [I have also included some historical observations from previous years that I can document with photos, but for which I cannot include the duration of each observation].

Some of the trees were more isolated than others, and in somewhat different environments. This not only influenced which species of birds might be feeding on a specific tree, but also how easy it was to note departure times, in particular, and sometimes even if a bird had fed. In all but one of my sites, the trees studied were not next to or very close to any other trees of the same species. The exception was in the "woods above

the cemetery" where a number of *Huevos de Caballo*trees had grown together. Unfortunately, some of these trees in that location that had historically been used by different species had been cut down prior to when I began my study, leaving many fewer trees to attract birds at that site. Finally, as Gumbo Limbo fruits were no longer available toward the end of my study, I concentrated more on some of the *Huevos de Caballo* trees, and for the last part of the study concentrated on one particular *Huevos de Caballo* tree that was very close to my house.

*Gumbo Limbo (Bursera simaruba)*

Gumbo Limbo fruits are red, but are completely enclosed in fruit capsules and therefore not normally visible, unless the fruit capsule has opened on its own, or been opened by an animal. The fruit capsules grow in bunches on secondary branches. For my study I observed four different Gumbo Limbo trees (12 observations for a total of 382 minutes). All except for the cemetery and Steve's Gumbo Limbos, described below, were at least one kilometer distant from each other. A description of each and its environment follows, as well as the terminology I used to reference it.

Cecilia's Gumbo Limbo — This is one of a number of living fence posts along the main road, and close to my house. Traditionally, I have often seen numbers of birds feeding in it, and I have included two such historical observations in my analysis. Unfortunately, the tree's fruit in 2021 did not last long, so there is only one full observation of it that year. Thus, my analysis of this tree is based solely on three different observations, two of which are historical. It seemed to bear fruit earlier than other Gumbo Limbos, and my follow-up survey in 2022 indeed shows this is so (total of 30+ minutes).

Llano Grande Gumbo Limbo — This tree was the farthest from my house (about two and a half kilometers). On all but one date it was observed both on my outward and return trips to the Llano Grande bus stop (about three kilometers away). The tree is just past a large *quebrada*(ravine) through which a significant stream passes (that never dries up completely). The *quebrada* has many trees but these are not very close to the Gumbo Limbo. This tree is across the main road from the valley surrounding the *quebrada* and is at the base of a hilly pasture. While there are some bushes nearby, the tree is somewhat isolated and never had numerous branches. These factors made noting feeding and departure times easier. Across the road from this tree on the edge of the *quebrada* is a large tree in which Rose-throated Becards (*Pachyramphus aglaiae)* had a nest. Very heavy and constant truck traffic during the last part of this study, probably affected the comings and goings of birds at this site. Observations of this tree were made seven times (total of 233 minutes).

Cemetery Gumbo Limbo — This tree was situated at the edge of the cemetery and was at the highest elevation of all the Gumbo Limbo trees I studied (probably 900+ meters above sea level). Although relatively isolated, the tree itself has numerous intertwining branches, which somewhat diminished my ability to note all activity within it, especially departure times. However, this maze of branches also made it relatively easy for birds to find spots where they could stand and feed. Near the top of the tree the branches thinned out and I often observed larger birds that appeared to claim these branches for themselves. Observations of this tree were made three times (total of 87 minutes).

Steve's Gumbo Limbo — This tree was less than 50 meters down the road from the cemetery tree, and I only noticed birds feeding in it when they were doing major construction (laying water pipe) next to the cemetery, so I don't believe it was a favorite feeding tree. Some birds may also have been intimidated by a pair of Rose-breasted Grosbeaks (*Pheuticus ludovicianus* ) that dominated the cemetery tree the same day. Only one observation of this tree was made (total of 32 minutes).

*Huevos de Caballo (Tabernaemontana donnell-smithii)*

In contrast to Gumbo Limbo, the fruits (seed husks) of *Huevos de Caballo* that contain the "fruit" (arils containing seeds) that birds eat are large. Somewhat spherical to ovoid-shaped, the seed husks may be as much 7-10 cm long x 5-8 cm in diameter (Foster & McDiarmid 1983). The seed husks hang down from a branch and a seam opens along the bottom of the husk. Each husk contains many orange-red arils, each enclosing one seed.

[These arils are] highly nutritious (mean nutrient composition/g dry weight tissue = 7.9% ash, 63.9% lipid, 10.95% protein, 8.5% TCA-soluble carbohydrate, 8.3%structural carbohydrate).... Birds are the primary agents of seed dispersal.... In return, the aril of the fruit provides the birds with an estimated 16-25% of their daily energy expenditure as well as meeting a substantial portion of their requirement for nitrogen. The peak of fruit ripening falls in the late dry season. (Foster & McDiarmid 1983: 329).

For my study I observed three different *Huevos de Caballo* sites. All three sites were at least one kilometer distant from each other. I made 26 different observations of these trees for a total of 930 minutes in 2021 and included six additional historical observations. A description of each site/tree and its environment follows, as well as the terminology I used to reference it.

Main road *Huevos de Caballo* —Although this was not the only*Huevos de Caballo* on the main road, it was the one I passed on my way into town. Unfortunately, this tree is in the middle of a number of other trees and thus at times difficult to observe well, especially since it was often full of foliage. Nevertheless, I had made significant observations of this tree in the past [most notably watching a Montezuma Oropendola (*Psarocolius montezuma* ) feed its fruit to a young Giant Cowbird (*Molothrus oryzivorus* )], and thus have included some historical records in my analysis. I often passed this tree on my way to other sites so some of my observations were shortened or not as detailed. My analysis will include seven observations of this tree, two of which are historical (total of 160+ minutes).

"Woods above the cemetery" *Huevos de Caballos* — Just past the cemetery is a small path that leads past an abandoned house to what used to be a small grove of these trees, and I had in the past found these were favored fruiting trees of many species of birds. Unfortunately, as noted above, the owner reopened the house and cut down some of the*Huevos de Caballo* trees that were on the path. While some still remained they were less accessible/visible. My analysis will include five observations of these trees, four of which are historical (total of 21+ minutes).

Willy's *Huevos de Caballo* — This tree was also located on the main road but further from town than my house. Although I had walked by it many times, I only recognized it as a *Huevos de Caballo* when I observed birds feeding on its fruits on March 22, more than two weeks after I had begun my study. [I had been focused on observing Cecilia's Gumbo Limbo, which was about fifty yards away from it on the other side of the main road, until it had ceased producing fruit]. The tree also had a number of branches but did not have as much foliage as the other*Huevos de Caballo* on the main road. It also at times had many husks containing seeds covered with fruit but I never saw more than four open at one time. There were trees on either side of it which were often used by birds as they flew back-and-forth to feed on its fruits. During the time I observed it, it appeared to have two separate "flowerings." Each time Plain-capped Starthroats (*Heliomaster constantii* ) were observed feeding on the tubular flowers. The tree was about a ten-minute walk from my house, and since I passed it on one of my longer walks, I sometimes had two observations on the same morning. As mentioned above, towards the end of the study, this tree was the only one I was observing. I made 20 observations of this tree (total of 755 minutes).

**Observation procedure**

Whenever I observed a bird fly into a fruiting tree, I noted the species and its time of arrival. I then watched the bird to see if it fed, and when possible noted when it left the tree or when I noticed the bird was no longer present. I did not generally note how many fruits a bird ate in one visit. Each observation only notes the presence of a bird and whether it fed or was not observed doing so during that visit. Each bird arrival was counted separately as one observation.

**T** his methodology led to understatement of the actual number of fruits consumed by some of the species. The best example of this can be seen by looking at my records of Fiery-billed Aracari (*Pteroglossus frantzii* ) feeding in Willy's *Huevos de Caballo* . Although my original records noted it only fed one time in that tree and was in the tree from 7:58-8:01 AM, a video I took of that bird showed that it grabbed 18 "fruits" (arils) one at a time in that time-span. Some other large birds also ate numerous fruits in one visit, while most smaller birds, which were generally in a tree for shorter periods, usually only grabbed one fruit at a

time. Given the variability, it is clear there were more actual feedings than my tables show.

I constructed two tables (Appendices 1and 2, which can be found at https://doi.org/10.5061/dryad.n5tb2rc0q) which included all my visits to each tree, and showed the total number of visits by each species, its arrival and departure times (if noted), and whether or not it fed.

## 3. RESULTS

2021**:** Overall, from 7 March to 9 April, birds were observed visiting Gumbo Limbos 146 times and fed on 102 of those visits. Similarly, from 5 March to 12 May, birds were observed visiting*Huevos de Caballos* 360 times and fed on 293 of those visits. Forty-two of the 115 different species I observed in April were observed feeding on the fruits of one or the other (Jackson 2021).

[2022: from 26 January to 7 March, I made seventeen observations (518 minutes) of two of the three Gumbo Limbo trees observed in the 2021 study and seven observations (245 minutes) of the same *Huevos de Caballo* trees observed in 2021. Birds visited Gumbo Limbos 360 times and fed on 191 of those visits; they also visited *Huevos de Caballos* sixty-two times and fed a maximum of thirty-eight times. As previously noted, the 2022 data (summarized in Appendix 3, which can be found at https://doi.org/10.5061/dryad.n5tb2rc0q) will not be used in this analysis, but will be referred to in the Discussion].

### 3.1 Birds visiting both fruiting trees

In my 2021 study, each tree species was visited by thirty-one species of birds, and twelve of those species visited both fruiting trees. However, of those twelve, eight species visited one of those trees much more frequently (>75% of visits), and eleven species spent more than 60% of their total number of feedings in one of them.

Of the four species that did visit both trees more frequently, two had very few visits — Boat-billed Flycatcher (*Megarynchus pitangua* ) with two visits, and Ochre-bellied Flycatcher (*Mionectes oleagineus* ) with four visits. However, two other species had more visits. Great Kiskadee (*Pitangus sulphuratus* ) visited*Huevos de Caballo* seven times and Gumbo Limbo five times, and Chestnut-capped Warbler (*Basileuterus delattri* ) visited*Huevos de Caballo* fifteen times and Gumbo Limbo eleven times. Nevertheless, both birds fed more frequently on one of the trees. Great Kiskadee fed on *Huevos de Caballo* fruits on 70% of its total feedings, whereas Chestnut-capped Warbler fed on Gumbo Limbo fruits on 77% of its total feedings.

[The 2022 study showed that both Ochre-bellied and Boat-billed Flycatchers fed much more frequently on Gumbo Limbo earlier in the year]. Thus, it is clear that even for those species that fed on both trees, one tree's fruit was clearly favored as a food resource.

### 3.2 Birds visiting Gumbo Limbo

As summarized in Appendix 1, of thirty-one bird species observed in Gumbo Limbos twenty-seven were observed feeding. Fifteen species fed at both the Llano Grande and the cemetery trees, nine species fed at Cecilia's tree, and five species fed at Steve's tree. Most visits were of short duration (one-two minutes), but several medium-sized birds did stay in the tree for longer periods of time. However, the bird with the fourth largest average time of visits, Red-legged Honeycreeper (*Cyanerpes cyaneus* ), was one of the smallest. No species was observed in all four Gumbo Limbos, but Rose-throated Becards (*Pachyramphus aglaiae* ), Yellow-green Vireos (*Vireo flavoviridis* ), and Yellow-throated Vireos (*Vireo flavifrons* ) fed in three of the four different trees. Also observed in three different trees were Dusky-capped Flycatchers (*Empidonax oberholseri* ), but they only fed in two of them.

However, of all the birds feeding on Gumbo Limbo fruits, the species observed the most was Scarlet-rumped Tanager (*Ramphocelus passerinii* ). Males and/or females fed in the Llano Grande Gumbo Limbo on six of the seven observations I made of this tree. During those observations, Scarlet-rumped Tanagers fed fifteen different times, and only on the last observation did Scarlet-rumped Tanagers visit but not feed. The only other species that fed frequently at the Llano Grande Gumbo Limbo were Chestnut-capped Warblers and

Red-legged Honeycreepers. Chestnut-capped Warblers fed seven times, and Red-legged Honeycreepers fed six times.

During my study eight migrant species were observed in the four different Gumbo Limbos. Only two did not feed on the fruits — Tennessee Warbler (*Leiothlypis peregrina* ) and Western Tanager (*Piranga ludoviciana* ). In comparison, twenty-four non-migrants/breeders visited these trees and only three were not observed feeding — Brown-crested Flycatcher (*Myiarchus tyrannulus* ), Boat-billed Flycatcher, and Gray-crowned Yellowthroat (*Geothlypis poliocephala* ).

### 3.3 Birds visiting *Huevos De Caballo*

As summarized in Appendix 2, during thirty-two visits a total of thirty-one bird species were observed in *Huevos de Caballo* trees. Twenty-four fed on the fruits/seeds; there were also two hummingbirds and five species did not feed on the fruit. Twelve species fed on the Main Street tree in seven visits (two visits are historical); eight species fed in the woods above the cemetery trees in five visits (four visits are historical); and nineteen species fed in Willy's tree in twenty visits. Four different species — Hoffman's Woodpecker (*Melanerpes hoffmanii* ), Red-legged Honeycreeper, Rufous-naped Wren (*Campylorhynchus rufinucha* ), and Yellow-green Vireo — were observed feeding at all three sites.

Of the thirty-one species observed in *Huevos de Caballo* , only five were classified as migrants. Two of them — American Redstart (*Setophaga ruticilla* ) and Rufous-tailed Hummingbird (*Amazilia tzacatl* ) did not feed on either the fruit or the flowers. The other three only fed on a few occasions — Summer Tanager (*Piranga rubra* ) - (1 time); Baltimore Oriole (*Icterus galbula* ) - (3 times); and Yellow Warbler (*Setophaga petechia* ) - (3 times). However, Yellow Warbler was observed in the trees eight other times (possibly hunting for insects).

## 4. DISCUSSION

### 4.1 Size analysis of birds visiting Gumbo Limbo

It has been argued that a limiting factor as to whether a bird can feed on a certain fruit relates to morphology and specifically the size of a species' bill (Wheelwright et al.1984, Moermond and Denslow 1985, Levy 1987, Jordano 1986, 2014, and Bender et al. 2018). Since Gumbo Limbo fruits are encased in an outer shell the questions arise: Does the size of a bird's bill determine whether it can feed on this particular fruit, and is it able to open its seed capsule and/or swallow the fruit inside? To analyze this I divided the species visiting these trees into two different categories of size: medium vs small (small being <15 cm), and arranged them in order of size (Garrigues and Dean 2014). These results can be seen in Table 1.

Table 1. Birds Visiting Gumbo Limbo

| Medium (>15 cm) | O | A | F | Small (<15 cm) | O | A | F |
|---|---|---|---|---|---|---|---|
| Boat-billed Flycatcher (BOBF)[23] | 1 | ? | - | Gray-capped Flycatcher (GCAF)[15] | 3 | 1.0 | 3 |
| Great Kiskadee (GKIS)[23] | 5 | ? | 3 | Piratic Flycatcher (PIRF)[15] | 7 | 3.6 | 5 |
| Brown-crested Flycatcher (BCFL)[20] | 1 | ? | - | Yellow-bellied Elaenia (YBEL)[15] | 1 | ? | 1 |
| Sulfur-bellied Flycatcher(SBFL)[20] | 1 | ? | 1 | Social Flycatcher (SOFL)[15] | 4 | 1.0 | 4 |
| Streaked Flycatcher (STFL)[20] | 4 | 6.5 | 3 | Yellow-green Vireo (YGVI)[15] | 4 | 1.0 | 2 |
| Tropical Kingbird (TRKI)[20] | 8 | 5.8 | 5 | Scarlet-rumped Tanager (SCRT)[15] | 21 | 2.4 | 15 |
| Black-crowned Tityra (BCRT)[20] | 7 | 8.5 | 2 | Dusky-capped Flycatcher (DCFL)[15] | 5 | 1.0 | 3 |
| Masked Tityra (MATI)[20] | 1 | ? | 1 | Yellow-throated Vireo (YGVI)[13] | 4 | 1.7 | 2 |
| Buff-throated Saltator (BTSA)[20] | 3 | 1.0 | 3 | Philadelphia Vireo (PHVI)[13] | 4 | 2.0 | 2 |
| Rose-breasted Grosbeak (RBGR)[20] | 9 | 21.7 | 7 | Gray-crowned Yellowthroat (GCYE)[13] | 2 | 1.0 | - |
| Hoffmann's Woodpecker (HOWO)[18] | 2 | 3.5 | 2 | Tennessee Warbler (TEWA)[13] | 1 | 1.0 | - |
| Rose-throated Becard (RTBE)[18] | 10 | 1.9 | 7 | Chestnut-capped Warbler (CCWA)[13] | 11 | 1.0 | - |
| Rufous-naped Wren (RNAW)[18] | 8 | ? | 8 | Yellow Warbler (YEWA)[13] | 4 | 2.0 | 2 |
| Western Tanager (WETA)[18] | 1 | ? | - | Ochre-bellied Flycatcher (OBFL)[13] | 2 | ? | 1 |

| | | | |
|---|---|---|---|
| Red-legged Honeycreeper (RLHO)[10] | 7 | 5.0 | 6 |
| South'n Beardless Tyran'let (SOBT)[10] | 1 | 3.0 | 1 |
| North'n Beardless Tyran'let (NOBT)[10] | 2 | 2.0 | 2 |
| Blue-black Grassquit (BGRA)[10] | 2 | 2.0 | 1 |

O — Total number of observations

A — Average amount of time per visit (minutes)

F — Number of feeding observations

The table shows that to some degree, size may have been a factor in the average amount of time spent in the tree on each visit. Some of the larger birds spent considerable time in the tree. My recollection, notes, and photos I took indicate that for some species, e.g. Rose-breasted Grosbeak (*Pheuticus ludovicianus* ), multiple feeding (constantly consuming one fruit after another) occurred in each visit. Other species, such as Tropical Kingbird (*Tyrannus melancholicus* ), used the tree more for perching than eating. However, even if larger birds may have monopolized "favorite" fruits, they did not prevent smaller birds from feeding as there were always many fruits to feed on.

However, the data do not suggest that smaller birds had more difficulty obtaining the fruit from the seed capsules. Apparently, the seed capsules, when ripe, are not sufficiently hard to be a factor in the amount of feeding by smaller birds on Gumbo Limbo fruits. It has also been previously noted that the fruit valves separate easily when ripe (Scott 1984).

[ In (2022) I observed two different ways by which birds removed the fruit from the seed capsule. A Gray-capped Flycatcher (*Myiozetetes granadensis* ) simply pulled the fruit out of its casing and swallowed the fruit. In contrast, a Social Flycatcher (*Myiozetetes similis* ) seemed to take more time: it grabbed the fruit in its beak and knocked it against a branch to remove half of the casing. It then proceeded to knock it against a branch again to remove the other half of its casing, before swallowing the fruit whole. The different techniques used in removing the fruit valve may have been related to the ripeness of the fruit (Pers. obs. 2/18/22)].

[My 2022 study showed the importance of Gumbo Limbo as a food resource during the dry season. Eight species (Masked Tityra (*Tityra semifasciata* ), Ochre-bellied Flycatcher, Brown-crested Flycatcher, Boat-billed Flycatcher, Great Kiskadee, Social Flycatcher, Gray-capped Flycatcher, and Tropical Kingbird) fed a total of 127 times in 2022, as opposed to 18 feedings in 2021].

### 4.2 Competition for resources in Gumbo Limbo

Another way in which size is a factor is that larger birds often chase off smaller birds, especially if there is limited fruit available. As there were generally large numbers of fruiting capsules with edible fruit on Gumbo Limbo, this was less of a factor than I observed within*Huevos de Caballo* . Nevertheless, I observed two instances of interspecific antagonistic behavior in the Llano Grande Gumbo Limbo, and two instances in the cemetery Gumbo Limbo. In all but one case the larger bird was the aggressor, with the exception being between birds of the same size. Since Piratic Flycatcher (*Legatus leucophaius* ) is by its nature pugnacious (it harasses other birds until they give up their nests), it is not surprising that it was antagonistic toward a bird of similar size. [As I recollect, these antagonistic behaviors did not always dislodge the target from the tree, but only caused it to move to another branch]. These results are summarized in Table 2.

Table 2. Antagonistic Behaviors in Gumbo Limbo

| Tree and date | Aggressor | Target |
|---|---|---|
| Llano Grande - 3/7/21 | Piratic Flycatcher (PIRF) [15] | Social Flycatcher (SOFL) [15] |
| Llano Grande - 3/16/21 | Hoffmann's Woodpecker (HOWO) [18] | Scarlet-rumped Tanager (SCRT) [15] |
| Cemetery - 3/9/21 | Sulfur-bellied Flycatcher (SBFL) [20] | Piratic Flycatcher (PIRF) [15] |

### 4.3 Size analysis of birds visiting *Huevos de Caballo*

While the four dominant species — Hoffmann's Woodpecker, Red-legged Honeycreeper, Rufous-naped Wren, and Yellow-green Vireo made constant visits back-and-forth to feed on the fruits, some of the larger birds stayed in *Huevos de Caballo* for much longer periods of time to continue feeding. I have already mentioned a Fiery-billed Aracari that I videoed taking at least eighteen fruits (one at a time) in succession. Similarly, Groove-billed Ani (*Crotophaga sulcirostris* ), White-winged Dove (*Zenaida asiatica* ), Keel-billed Toucan (*Ramphastus sulfuratus* ), Lesson's Motmot (*Momotus lessonii* ), Pale-billed Woodpecker (*Campephilus guatemalensis* ), Great Kiskadee, and Clay-colored Thrush (*Turdus grayi* ) spent longer times in a tree. While larger birds also did this in Gumbo Limbos, given the relatively scarcity of fruit to be had in *Huevos de Caballo* trees (at most four different seed husks might be open at one time on a tree), these larger birds showed much more antagonism toward the smaller birds, and sometimes even toward birds of similar size. At times the competition for fruit even caused small birds to chase other small birds. However, even if these larger birds did not exhibit antagonistic behavior, by situating themselves on a branch either over or under an opened husk, they monopolized that fruit for as long as they were there.

In Table 3 I have divided the birds by size using the same criteria as I did above (i.e., larger or smaller than 15 cm) for the birds visiting Gumbo Limbo. I have also arranged them by actual size as is shown by their length in centimeters within the brackets (Garrigues and Dean 2014). Several things stand out when looking at Table 3 in terms of the size of the birds observed visiting *Huevos de Caballo* . The first and most obvious is that almost twice as many birds that visited*Huevos de Caballo* were medium-sized (larger than 15 cm), and at least two (Keel-billed Toucan and Montezuma Oropendola) might well be considered "Large." The second is that three of the medium-sized birds (White-winged Dove, Clay-colored Thrush, and Rufous-naped Wren) and two of the small birds (Yellow Warbler and Chestnut-capped Warbler) visited many more times than they fed. In contrast, three of the medium-sized birds (Keel-billed Toucan,

Table 3. Birds Visiting *Huevos de Caballo*

| Medium (>15 cm) | O | A | F | Small (<15 cm) | O | A | F |
|---|---|---|---|---|---|---|---|
| Keel-billed Toucan (KBTO) [46] | 4 | 2.5 | 7 | Dusky-capped Flycatcher (DCFL) [15] | 1 | 1.0 | - |
| Montezuma Oropendola (MORO) [46] | 8 | 1.0 | 8 | Yellow-green Vireo (YGVI) [15] | 56 | 2.2 | 51 |
| Pale-billed Woodpecker (PBIS) [33] | 5 | 9.3 | 3 | Blue-gray Tanager (BGTA) [15] | 1 | ? | - |
| Groove-billed Ani (GBAN) [30] | 11 | 2.7 | 7 | Scarlet-rumped Tanager (SCRT) [15] | 2 | 2.0 | 2 |
| Giant Cowbird (GICO) [28] | 1 | ? | 1 | Ochre-bellied Flycatcher (OBFL) [13] | 2 | ? | 2 |
| White-winged Dove (WWDO [28] | 29 | 5.8 | 11 | American Redstart (AMRE) [13] | 1 | ? | - |
| White-tipped Dove (WTDO) [28] | 1 | ? | - | Yellow Warbler (YEWA) [13] | 12 | 1.8 | 3 |
| Boat-billed Flycatcher (BOBF) [23] | 1 | 2.0 | 1 | Chestnut-capped Warbler (CCWA) [13] | 15 | 1.8 | 3 |
| Clay-colored Thrush (CCTH) [23] | 37 | 1.4 | 17 | Red-legged Honeycreeper (RLHO) [10] | 46 | 5.9 | 41 |
| Great Kiskadee (GKIS) [23] | 7 | 2.2 | 6 | Yellow-faced Grassquit (YFGR) [10] | 1 | 2.0 | - |
| Grayish Saltator (GRAS) [20] | 2 | 1.0 | 1 | | | | |
| Baltimore Oriole (BAOR) [20] | 3 | 1.0 | 3 | | | | |
| Hoffmann's Woodpecker (HOWO) [18] | 53 | 1.2 | 50 | | | | |
| Rufous-naped Wren (RNAW) [18] | 50 | 2.1 | 36 | | | | |
| Summer Tanager (SUTA) [18] | 1 | ? | 1 | | | | |
| Rose-throated Becard (RTBE) [18] | 1 | 1.0 | 1 | | | | |
| Fiery-billed Aracari (FBAR) [17] | 5 | 2.0 | 22 | | | | |
| Lesson's Motmot (LEMO) [16] | 6 | 4.9 | 19 | | | | |

O — Total number of observations

A — Average amount of time per visit (minutes)

F — Number of feeding observations

Fiery-billed Aracari, and Lesson's Motmot) had more observed feedings than visits. [This anomaly is due to the fact that, towards the end of the study, for these medium-sized species I had noted how many different times they had fed during a particular visit]. The third observation we can make from the table is that, overall, there does not seem to be much of a correlation between the size of the bird and the average amount of time it spent on each visit to a *Huevos de Caballo* . The average time for each medium-sized bird was 2.7 minutes, and for small birds it was 2.4 minutes. In contrast, the averages for birds visiting Gumbo Limbo were 7.0 minutes for medium-sized birds and 1.9 for small birds.

Table 4. Antagonistic Behaviors in *Huevos de Caballo*

| Date and tree | Aggressor | Target |
|---|---|---|
| Main road - 3/6/21 | Pale-billed Woodpecker (PBIS) [33] | Red-legged Honeycreeper (RLHO) [10] |
| Main road - 4/9/21 | Lesson's Motmot (LEMO) [16] | Hoffmann's Woodpecker (HOWO) [18] |
| Main road - 4/9/21 | Lesson's Motmot (LEMO) [16] | Baltimore Oriole (BAOR) [20] |
| Willy's - 4/11/21 | Keel-billed Toucan (KBTO) [46] | White-winged Dove (WWDO) [28] |
| Willy's - 4/15/21 | Keel-billed Toucan (KBTO) [46] | Hoffmann's Woodpecker (HOWO) [18] |
| Willy's - 4/20/21 | Red-legged Honeycreeper (RLHO) [10] | Yellow-green Vireo (YGVI) [15] |
| Willy's - 4/21/21 | Groove-billed Ani (GBAN) [30] | Rufous-naped Wren (RNAW) [18] |
| Willy's - 4/21/21 | Groove-billed Ani (GBAN) [30] | Hoffmann's Woodpecker (HOWO) [18] |
| Willy's - 4/22/21 | Great Kiskadee (GKIS) [23] | White-winged Dove (WWDO) [28] |
| Willy's - 4/22/21 | Great Kiskadee (GKIS) [23] | Clay-colored Thrush (CCTH) [23] |
| Willy's - 4/22/21 | Groove-billed Ani (GBAN) [30] | Lesson's Motmot (LEMO) [16] |

### 4.4 Competition for resources in *Huevos de Caballo*

In Table 4 I have noted the number of antagonistic observations that were made, the aggressor and the target, and again noted the length of each bird in brackets. As previously noted, in *Huevos de Caballo*the number of seed husks that contained edible (and accessible fruit) was limited at any time. Thus, it could be expected that antagonisms and competition would be more

frequent. There were indeed more frequent instances of antagonism, and in most instances the aggressor was the larger bird. However, there were four instances where the aggressor was smaller — both antagonisms by the Lesson's Motmot, the antagonism of Great Kiskadee toward White-winged Dove, and the antagonism by Red-legged Honeycreeper toward Yellow-green Vireo. There was also one instance in which the aggressor and recipient were the same length.

While there were more antagonisms in the *Huevos de Caballos* I studied, nevertheless given that out of 299 feeding observations I observed only 11 instances of antagonism and displacement, they were still comparatively rare. In this respect my observations are consistent with those made by McDiarmid et al. (1977) that interspecific displacements are rare.

While one might impute these antagonisms to the relative belligerence of each species (some flycatchers are known to be especially pugnacious), there might be an alternative explanation. Looking at Table 4 and back to my notes, I find that after the Yellow-green Vireo had fed it was chased by a pair of Red-legged Honeycreepers, which subsequently fed themselves (presumably on the same fruits). Thus, it took two birds to dislodge one. In the two cases of Lesson's Motmot aggressive behavior, which occurred on the same day, the motmot chased away the Hoffmann's Woodpecker, after the woodpecker had fed; later, while it was itself feeding, the motmot chased away a Baltimore Oriole which flew in attempting to feed. The first situation of the Great Kiskadee is even more complicated. According to my notes, both the White-winged Dove and the Great Kiskadee had been feeding (presumably on different fruits) prior to the altercation. With regard

to the antagonistic behavior toward the Clay-colored Thrush, the Great Kiskadee had been feeding before it chased the Clay-colored Thrush away. Thus, excepting the situation where a pair of birds dislodged a larger bird, there does not seem to be enough evidence to support an alternative explanation, other than that of an innate belligerence of a species, although further study is clearly needed.

[ On March 3, 2022 I observed intraspecific antagonism. A female Red-legged Honeycreeper was perched on a hanging (vertical) branch, which enabled it to reach sideways and feed on an opened*Huevos de Caballo* fruit. When a second female Red-legged Honeycreeper came down the branch to also feed from that fruit, the first female aggressively chased it away. This is the only intraspecific antagonism I ever noted in either tree].

### 4.5 Importance of size overall

From my observations it appears that size is an important factor in determining which species gets to feed on fruit, only if the amount of fruit that is edible and/or accessible is limited. Given that the two species of trees I studied have very different fruiting strategies (abundant fruit available throughout the tree vs limited fruit being available sequentially), one might surmise that the size of a bird is more of a major factor in its success in feeding on fruits that are made available sparingly. However, one would have to examine many other species to see if that statement holds true, or whether bird feeding behavior in the fruiting trees I observed is an anomaly.

A second tentative conclusion can also be made. For both tree species larger birds could consume more than one fruit at a time, and often did so. Thus, it seems that my observations support the thesis that consumption of fruit is positively correlated with body size (Jordano 1986). One other possible explanation for the disparity in size between birds visiting the two trees is that larger-sized birds have higher energy needs which accounts for the relative difference in size between birds eating *Huevos de Caballo* fruits (lipid-rich) and those eating fruits of Gumbo Limbo (lipid-poor).

### 4.6 Lipid-rich fruits vs lipid-poor fruits

In their 2020 paper "Frugivory Specialization in Birds and Fruit Chemistry Structure Mutualistic Networks across the Neotropics" Pizo et al. analyzed 84 different studies of birds visiting various fruiting trees to feed. They also analyzed the different fruiting trees to determine whether their fruits were lipid-rich or lipid-poor, then charted the results to show which species were feeding on specific types of fruit and discussed how those feeding behaviors might ultimately affect seed dispersal of various plants. While my study only looked at two species of plants, their analysis shows that the family of one, Gumbo Limbo (*Burseraceae* ), is very low in lipids and high in sugars, while the family of the other, *Huevos de Caballo*(*Aponcynaceae* ), has one of the highest percentages of lipids in the fruit pulp. Thus, I thought it would be interesting to relate my findings to theirs regarding species feeding on these two different families. The results of these comparisons can be seen in Table 5 and Table 6. The order of each table is determined by the number of observations in which the species is noted feeding.

The Pizo study concluded that the family of flycatchers ( *Tyrannidae* ) plays a major role in seed dispersal of fruiting trees in the tropics, and a recent study of *Bursera* tree species showed that family to be their major seed dispersers (Almazan-Nuñez 2016). Table 5, at first glance, seems to show the *Thraupidae*family feeding on Gumbo Limbo the most. However, if we combine all the observations of members of *Tyrannidae* , we find in fact that the percentage of both total observations of that family (32%) and observations when feeding was observed (37%) are larger than the amounts combined for members of *Thraupidae* (20% of total observations and 21% of observations when feeding was observed). Pizo's study also found that the highest amount of frugivory was by members of the *Thraupida* e family with members of *Tyrannidae* being second. Thus, at least with regard to Gumbo Limbo, both our studies show these families to be the most frugivorous in the neotropics.

Despite this general agreement between our studies, I observed significant feeding activities in Gumbo Limbo by four members of bird families, which were not observed doing so in the studies analyzed by Pizo. These four

species were Rose-breasted Grosbeak, Chestnut-capped Warbler, Rufous-naped Wren, and Rose-throated Becard. The extent of their feeding activities in Gumbo Limbo can be seen in Table 5. However, it is probable that the activities of Rose-breasted Grosbeak are undercounted. Like some other medium-sized species, Rose-breasted Grosbeak was a species that often fed numerous times each time it flew into a Gumbo Limbo. As evidenced both by photos and my own recall, it fed on these fruits many more times than the seven times indicated in the table.

Likewise, Table 6 (Birds Visiting *Huevos de* Caballo) shows more differences between my observations and the ones cited in Pizo et al. Overall, there were many fewer visits to this family of fruiting trees (*Apocynaceae* ) by birds in their studies. I also observed eight species of birds from bird families not observed feeding on the fruits of this family in their study. Five of those species (Rufous-naped Wren, Fiery-billed Aracari, White-winged Dove, Keel-billed Toucan and Groove-billed Ani) were observed feeding multiple times, and the number of their feedings were probably also undercounted due to my methodology.

What might account for these differences between my study and theirs? One might be the time of year when the studies were conducted. My studies were conducted at the beginning of the rainy season, when many species in my area are beginning to reproduce. Another occurrence at this time of year is that migrants are starting to move north. Could this possibly have influenced the great amount of feeding done by Rose-breasted Grosbeak on Gumbo Limbo fruits? A third possibility is that some species (either birds and/or trees), which are common where I live, are less common and/or absent from the areas where other studies were conducted.

### 4.7 Reproduction and feeding behavior

Given the number of feeding visits to the Llano Grande Gumbo Limbo by both male and female Scarlet-rumped Tanagers, I am certain they had a nest nearby and were feeding the fruits to their young. I also once saw either a female or young Scarlet-rumped Tanager sitting hidden underneath a bush right next to this tree. [After reading Skutch's account of fledged Scarlet-rumped Tanager behavior, I now wonder if what I saw was indeed their fledgling (Skutch 1980)]. This was also the only Gumbo Limbo where I observed Scarlet-rumped Tanager. Scarlet-rumped Tanagers are very common birds, so their absence in other trees indicates Gumbo Limbo fruits are not a major food resource for them. Their presence in only this tree is further indication that they were feeding young. Either they took advantage of a convenient food source to feed their chicks, or perhaps the high sugar and lipid-poor content of Gumbo Limbo may have met the nutritional needs of its young, but not have been needed by the adults.

McDiarmid et al. (1977) surmised that the arils of *Huevos de Caballo* may not be a suitable food for young birds. The basis of their assumption was that in only five of ninety-six observations of Hoffmann's Woodpeckers feeding their young had the young been fed the arils of that fruit. Unlike theirs, my observations suggest that the lipid-rich arils of *Huevos de Caballo* may be an important nutritional need of several species of newly-hatched birds, specifically Hoffmann's Woodpecker, Yellow-green Vireo**,** and Rufous-naped Wren.

I made fifty observations of feeding done by Hoffmann's Woodpecker with forty-four done at Willy's *Huevos de Caballo* . As previously noted, there was at least one nest hole of Hoffmann's Woodpecker close by. I observed both males and females fly in, grab one of the "fruits" (arils) and immediately fly off. On 11 April 2021, adults flew in and grabbed fruit eight times in an hour, and on 15 April 2021, they did this nine times within a half-hour. Several of those times I followed the bird to its nest hole and observed the young being fed, and I assume it was also being fed on those occasions when I did not follow the bird.

I also saw fifty-one instances of feeding being done by Yellow-green Vireos, with forty done in Willy's *Huevos de Caballo* . From 11 April to 15 April I observed 23 different feedings in this tree. Birds arrived to feed both singly and in pairs, and like the Hoffmann's Woodpecker, the birds flew in and out grabbing fruits constantly. Although I did not see a Yellow-green Vireo nest near this tree, given this concentration of feeding behavior, I suspect there was a nest nearby.

Finally, I observed twenty-nine similar instances of feeding by Rufous-naped Wren in Willy's *Huevos de*

*Caballo.* As Rufous-naped Wren is a very common species that nests in gardens, it is likely there were many nests and young nearby. Again, the frantic feeding behavior of the adults was similar to that of Hoffmann's Woodpeckers, which led me to believe they too were feeding young.

What might account for the differences between my observations and those made by McDiarmid, especially with respect to Hoffmann's Woodpeckers? My observations of Hoffmann's Woodpecker feeding on Willy's *Huevos de Caballo* were made over a period of over a month (25 March to 29 April) with the greatest number of feedings from 11-15 April. In contrast, Mc Diarmid's observations at the Hoffmann's Woodpeckers' nest site were done on one day, 25 April. Could it be that the young they observed being fed were at a stage where insect protein was a more important food source for them? It may be that earlier in their development the young are more in need of lipid-rich nutrients. Alternatively, perhaps there were insufficient quantities of insects during the earlier period of my observations, and the Hoffmann's Woodpecker were substituting a readily available food resource.

In conclusion both Gumbo Limbo and *Huevos de Caballo* are important food resources in the neotropics for both frugivorous and insectivorous species of birds. Gumbo Limbo fruits are high in sugar content, and consumed by many normally insectivorous birds and migrants, and as my 2022 study shows, the tree is especially important as an energy source toward the end of the dry season when other trees are not in fruit. In contrast, *Huevos de Caballo* provides fruits high in lipids which many larger and mostly resident birds consume. Both trees also seem to be important sources of nutrition for young birds during their development and help to maintain bird diversity in populated areas. The continued use of Gumbo Limbo as living fences and cultivation of *Huevos de Caballo* should both be encouraged to maintain bird diversity in areas of human habitation.

## ACKNOWLEDGEMENTS

I would like to thank Tomás Carlo, who sent me the study by Pizo et al., John Kricher, who made suggestions on how to modify this paper and the Abstract in particular, and Bridget Stutchbury, who commented on the section on reproductive behavior. I would also like to thank Pat Randall and Soheil Zendeh who both made editing suggestions.

## DATA AVAILABILITY STATEMENT

The data that support the findings of this study (Appendices 1, 2, & 3) are openly available in the Dryad Digital Repository at https://doi.org/10.5061/dryad.n5tb2rc0q.

## ORCID

**C** raig Leslie Jackson,

*https://orcid.org/0000-0002-3845-7968*

## REFERENCES

Almazán-Nuñez, R. C., L. E. Eguiarte, M. del Coro Arizmendi, and P. Corcuera. 2016. *Myiarchus* flycatchers are the primary seed dispersers of *Bursara longipes* in a Mexican dry forest. PeerJ 4:e2126; DOI 10.7717/peerj.2126.

Albrecht, J., J. Hagge, D. G. Schabo, H. M. Schaefer, and N. Farwig. 2018. Reward regulation in plant–frugivore networks requires only weak cues. Nature Communications 9, 4838 (2018). https://doi.org/10.1038/s41467-018-07362-z.

Bender, I. M. A., W. D. Kissling, P. G. Blending, K. Bohning-Gaese, I. Hensen, I. Kuhn, M. C. Muñoz, E. L. Neuschulz, L. Nowak, M. Quitián, et al. 2018. Morphological trait matching shapes plant–frugivore networks across the Andes. Ecography, Vol. 41, Issue 11 (November, 2018), pps 1910-1919. *https://doi.org/10.1111/ecog.03396* .

Carlo,Thomás. 2021. Effects of avian frugivory in the structure and resilience of plant communities. Zoom presentation to the Nuttall Ornithological Club, March 1, 2021.

Foster, M.S., and R.W. McDiarmid. 1983. *Stemmadenia donnell-smithii* (Hu*evos de Caballo,* Cojones de Chancho). pp 328-329 in Costa Rican Natural History, ed. by Daniel H. Janzen. University of Chicago Press, Chicago.

Garrigues, Richard and Robert Dean. 2014. The Birds of Costa Rica. 2nd Edition. A Zone Tropical Publication. Cornell University Press, Ithaca, N.Y.

Griscom, H. P., E. K. V. Kalko, and M. S. Ashton. 2007. Frugivory by small vertebrates within a deforested, dry tropical region of Central America. Biotropica, Vol. 39, No.2 (March 2007), pp. 278-282. Published By: Association for Tropical Biology and Conservation.

Jackson, C. L. 2021. https://ebird.org/lifelist?r=world&time=month&year=2021&m=4.

Jackson, C. L. 2023. Birds observed in and feeding on Gumbo Limbo and Huevos de Caballo, Dryad, Dataset,*https://doi.org/10.5061/dryad.n5tb2rc0q* .

Janzen, D. H., ed. 1983. Costa Rican Natural History. Chicago University Press. Chicago.

Jordano, P. 1987. Frugivory, external morphology and digestive system in mediterranean sylviid warblers Sylvia spp. Ibis, Vol.129, Issue S1, (January 1987), 175-189. https://doi.org/10.1111/j.1474-919X.1987.tb03199.x.

Jordano, P. 2014. Fruits and Frugivory. Chapter 2, 18-44. Seeds:

The Ecology of Regeneration of Plant Communities. Edition: 3. Ed. Gallagher R.S., CAB International.

Levy, D. 1987. Seed size and fruit-handling techniques of avian frugivores.

The American Naturalist, April 1987, Vol.129, No. 4.

Loiselle, B. A., and J. G. Blake. 1990. Diets of understory fruit-eating birds in Costa Rica: seasonality and resource abundance. Studies in Avian Biology, No. 13:9 1-103.

McDiarmid, R. W., R. E. Ricklefs, and M. S. Foster. 1977. Dispersal of Stemmadenia donnell-smithii (Apocynaceae) by birds. Biotropica, Vol. 9 No.1 (March, 1977), pps. 9-25. Published By: Association for Tropical Biology and Conservation.

https://www.jstor.org/stable/2387855.

Moermond, T. C. and J. Denslow. 1985. Behavior, morphology, and nutrition with consequences for fruit selection. Ornithological Monographs, No. 36, American Ornithologist's Union, pps 865-897. https://doi.org/10.2307/40168322.

Pizo, M. A., J. M. Morales, O. Ovaskainen, and T. A. Carlo. 2021. Frugivory specialization in birds and fruit chemistry structure mutualistic networks across the neotropics. The American Naturalist, Vol. 197, No. 2, February 2021, sent to me by Tomás Carlo.

Scott, P. E. and R. F. Martin. 1984. Avian consumers of Bursera, Ficus, and Ehretia fruit in Yucatan. Biotropica, Vol. 16, No. 4 (Dec., 1984), pps. 319-323 (5 pages). Published by: Association for Tropical Biology and Conservation.

Skutch, A. F. 1980. A Naturalist on a Tropical Farm. University of California Press, Los Angeles.

Snow, David. 1981. Tropical frugivorous birds and their food plants: a world survey. Biotropica, Vol. 13, No. 1 (March), pps. 1-14. Association for Tropical Biology and Conservation. https://doi.org/2387865.

Thornton, B. M., J. L. Knowlton, and W. A. Kuntz. 2015. Interspecific competition and social hierarchies in frugivororous neotropical birds in Costa Rica. Journal of Young Investigators, August 2015.

Wheelwright, N. T., W. A. Haber, K. G. Murray, and C. Guindon. 1984. Tropical fruit-eating birds and their food plants: a survey of a Costa Rican lower montane forest. Biotropica, Vol. 16, No. 3 (Sep., 1984), pp. 173-192 (20 pages). Published by: Association for Tropical Biology and Conservation.

Wilms, J.J.A.M., and M. Kappelle. 2006. Frugivorous birds, habitat preference and seed dispersal in a fragmented Costa Rican montane oak forest landscape. Ecological Studies, Vol. 185. Chapter 24, 309-324, in Kappelle, Maarten, ed. Ecology and Conservation of Neotropical Montane Oak Forests. 10.1007/3-540-28909-7.