Diversity, abundance, richness, and composition of avian communities and avian foraging behavior at *Ficus pertusa*

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ABSTRACT

This study investigated differences in success between fruiting *Ficus pertusa* trees in a single pasture in Monteverde, Costa Rica. Success was qualitatively measured by the abundance, richness and diversity of avian dispersers and the total number of seeds dispersed (as measured by the number of visits by birds that swallow fruits). Each of the four sites was observed for five days from 7:00am – 11:00 am. Significant differences in diversity were found in five of seven comparisons between the sites, but neither diversity nor number of bird visits was related to dbh or crop size of the tree. Significant differences were found in the number of swallowing birds at each site, affecting the dispersal success of each tree. Proximity to forest patches and crop size may affect the overall success of a tree and differences in success are due to the interaction of several factors that change over very small spatial scales.

RESUMEN

Este estudio investigo las diferencias del éxito entre cuatro *Ficus pertusa* con frutas en un potrero en Monteverde, Costa Rica. El éxito fue medido por la abundancia, la riqueza de especies y la diversidad de pájaros que comen frutas y también el número de las semillas dispersaron (medido por el número de visitas de pájaros que tragan frutas). Cada de los cuatro sitios fue observado por cinco días, de las siete hasta las once de la mañana. Diferencias significativas con la diversidad fueron encontradas en cinco de los siete comparaciones entre los sitios, pero ni la diversidad ni el numero de los visitas de pájaros estuvo correlacionado con el diámetro del arbol o el numero de las frutas en el arbol. Diferencias significativas fueron encontradas en el número de pájaros en cada sitio, afectando el éxito de cada arbol. Es posible que la proximidad a fragmentos de bosque y el número de frutas del arbol afecten el éxito del arbol. Diferencias en el éxito son causadas por la interacción de varios factores que cambian sobre espacios pequeños, afectando el éxito de un arbol.

INTRODUCTION

The genus *Ficus*, with over 900 species worldwide, is among the most widespread tropical genera (Janzen 1979). It is a keystone resource for many birds and mammals because trees produce fruits asynchronously throughout the year, guaranteeing a food source during the dry season (Janzen 1979, Terborgh 1986). Terborgh (1986) goes so far as to say that tropical ecosystems would collapse without the presence of fig trees.

All *Ficus* species have extremely large seed shadows due to the wide diversity of their dispersers (Janzen 1979, Jordano 1983). In Monteverde, Costa Rica, *Ficus* species receive a disproportionate number of frugivores when compared to other common genera

in Monteverde (Wheelwright, et al. 1984). They are thought to attract diverse and abundant dispersers because the seeds have no secondary compounds and they are a constant food source (Janzen 1979). Furthermore, because the fruits are soft, there is no limitation on the gape size of dispersers; animals can peck or mash the fruits, in addition to swallowing them whole (Janzen 1979, Wheelwright, 1985).

Ficus pertusa, the focal species in this study, is found in both forest and open areas and is common in pastures and fragments in Monteverde. It is either a hemiepiphyte or an independent tree and grows 10-15 meters tall. Populations fruit asynchronously and each tree produces a crop approximately once a year. Crop size varies from 100-200,000 fruits per tree and the fruiting period lasts between three weeks and three months (Bronstein and Hoffmann 1987). Fruits are dispersed by a variety of vertebrates, especially avian species, and are not dispersed by bats. (Bronstein and Hoffmann 1987, Dinerstein 1983 in Bronstein and Hoffmann 1987).

The foraging behavior of dispersers is one factor determining the overall success of F. persusa. Birds that peck at fruits are the least effective dispersers since they eat few, if any, seeds. Birds eating fruits by mashing disperse some seeds, however a large portion of each fruit is dropped below the parent tree, allowing little hope for germination. Swallowing birds are likely the best dispersers since they don't drop any seeds below the parent tree and disperse seeds through defecation at other locations. Peck was defined as the action of a bird foraging and eating a small part of the fruit without removing it from the tree. Mashing occurred when a bird removed a fruit from a tree and chewed it while perching, allowing some pieces of the fruit to fall to the ground. Swallowing was defined as the removal and ingestion of a whole fruit.

Spatial and temporal variations between trees are very important in determining the diversity, richness and composition of dispersers at *F. pertusa* (Bronstein and Hoffmann 1987). Temporal variation can be defined as changes between different times, such as seasons, and spatial variation is changes over an area such as ecosystems. This study investigated the differences in the successes of an individual tree without the influence of these two factors. Success was qualitatively measured by the total abundance of bird visits, the diversity and richness of dispersers and the quantity of seeds dispersed (as measured by the number of visits by swallowing birds).

MATERIALS AND METHODS

This study was conducted in the Monteverde region of Costa Rica (1450 meters), which is located on the northern Pacific slope of the Cordillera de Tilarán. One pasture was chosen for its abundance of *Ficus pertusa* trees planted for windbreaks and borders. Four tree sites with ripe fruit were selected in the pasture. Sites One, Two and Three were located beside each other in a line. Site One was continuous with a small forest patch. Site Four was located on the other side of the pasture, approximately 50 metes away and was growing in a windbreak of pine trees. Site One had two trees with their branches entwined, while sites two, three and four were single trees.

Data were collected from October 25, 2000 – November 12, 2000. Each site was observed for five days, from 7:00am – 11:00am and Sites One, Two and Three could be observed simultaneously due to their close proximity. During the observation periods, each bird was identified and the site and foraging behavior of the bird were noted. Foraging behavior was recorded as a peck, mash, swallow, glean, sally and/or perch.

The crop size of each site was estimated by counting the number of fruits on an accessible branch and multiplying it by the number of similarly sized areas on the tree. Diameter at breast height (dbh) was also measured at each site. Dbh was measured at Site One by adding the individual dbh of each tree and treating it as one measurement.

To analyze diversity, the abundance of each species was counted and the Shannon-Weiner Diversity Index (H') (Zar 1984) and Evenness were calculated for each site. A modified t-test on diversity was used to determine if differences between the sites were significant. Furthermore, Sorenson's Index was used to assess similarity of species composition between the sites. For both the t-test and Sorenson's index, pairwise comparisons were calculated between all sites. Also, Sites One, Two and Three were tested against Site Four to determine if birds see a close grouping of fruiting trees as a single target of food.

To analyze the relationship between bird species and foraging behavior the average weight of birds in the categories peck, mash and swallow was determined and compared using a one-way ANOVA. Furthermore, Chi-Square tests were used to compare the abundance of visits in all foraging categories and the abundance of the foraging categories peck, mash, and swallow between sites.

RESULTS

There was great variation in the number of visits, species richness and diversity between the four sites in the pasture (Table 1). Neither the number of visits nor diversity was related to crop size or dbh (Figures 1-4). However, Site One, with the largest tree and the largest crop size, had a far greater number of visits and species richness than the three smaller trees (57% of the 754 total bird visits and 18 of 22 recorded species). Further, there were significant differences in the diversity of avian species between all sites except Sites One and Four and Sites Two and Four (modified t-test, p – values $< .05$, Table 2). Also, when Sites One, Two and Three were tested as a single data point against site Four, there was significantly different diversity (p-value $< .001$, Table 2) (Zar, 1984).

When analyzing the similarity of species composition, pairwise comparisons between each site were calculated as well as a comparison of Sites One, Two and Three to Site Four. The values of Sorenson's index ranged from 0.50 to 0.71 and five of the seven comparisons gave values between 0.50 and 0.55, indicating that species composition changed little between the sites (Table 2). Similarity was not related to distance between the trees, i.e., trees located closer to one another did not show a greater similarity of species composition.

The differences between weights of bird in a foraging categories peck, mash and swallow were analyzed using a one-way ANOVA. The average weight of birds pecking,

mashing, and swallowing was 8.5 g, 20.8 g and 84.2 g, respectively. A significant difference (F-value = 959.39, df = 2, $p < .001$) between the average weight of birds in each category was found (Table 3).

Birds foraging for fruit comprised the majority of bird visits, with 745 (98%) of the 758 total bird visits. Frugivores also showed the greatest richness at *Ficus pertusa*, with 13 of the 17 species of identified birds. Birds gleaning, sallying, and perching were only 13 (2%) of the total bird visits and six species. (There was overlap between categories because Hoffman's Woodpecker was observed gleaning and swallowing and the Black-Throated Green Warbler was seen pecking and gleaning). A Chi Square was calculated between total number of visits of birds eating fruit and birds sallying, gleaning and perching and a significant difference was found ($X^2 = 1120.27$, df = 1, p-value < .01).

There were large differences in the behavior of frugivorous birds in *F. pertusa*. Birds pecking at the fruit comprised 57.6% of total bird visits. However, the species richness in this category was very low (s = 2) and Tennessee Warblers made up 99.8% of the total visits. Swallowing birds had the highest richness (s= 8) and comprised 26.0% of total visits while mashing birds comprised 14.6% of visits with a richness of four species. Using a Chi Square test a significant difference in number of bird visits was found between the three categories of frugivore behavior ($X^2 = 706.89$, df = 5, $p < .01$). There were also significant differences between the sites for the number of birds in each foraging category (peck: $X^2 = 248.8$, df = 3, $p < .001$; mash: $X^2 = 104.3$, df = 3, $p < .001$; swallow: = 112.1, df = 3, $p< .001$, Table 4). Site One and especially Site Three were dominated by Tennessee Warblers (pecking birds), although Site One also had a high number of swallowers. Site Two was more evenly distributed between the three foraging categories and Site Four was dominated by swallowing birds, such as Clay Colored Robins, Blue Crowned Motmots and Mountain Elaenias.

DISCUSSION

An individual trees' success can be measured by the abundance, richness and diversity of its dispersers, as well as the number of seeds dispersed. When combining these factors, Site One was the most successful tree. It had the highest abundance of visits (n = 368), the highest richness (s = 18) and relatively high diversity (H' = 0.704006). It also received the highest number of visits (n= 109) and richness (s = 8) of swallowing birds. There are many possible reasons for Site One's success. First, it was continuous with a small patch of forest. Some birds, such as the Blue-Crowned Motmot, were reluctant to cross open spaces and were found mainly in Sites One and Four (which was continuous with pine trees). Second, Site One was continuous with an orange tree and many birds were observed using both the *F. pertusa* and the orange tree.

Site Four also had a high measure of success. It had the highest diversity and a very high proportion of swallowing birds visited the tree (49 of 74 total visits). It did have a low number of bird visits, however, which may be due to its isolation from other fruiting *F. pertusa*. Birds were observed hopping between Sites One, Two and Three, but

this couldn't happen at Site Four. One possible explanation for its high diversity and number of swallowers is its proximity to pine trees, as explained above.

Site two had a much lower measure of success than both Sites One and Four. Although it was fairly even (E = .705), it had lower diversity. Twenty-nine of its 81 bird visits were from swallowers, a decent proportion, but a fairly low total number. Its total abundance was likely constrained by its size; there was not room for more than five or six birds on the tree at once. In contrast, Sites One and Three often had ten or more birds in their branches at one time.

The lowest success was found at Site Three. Despite its high number of total visits (n = 230), its overall diversity was extremely low (H' = 0.225745) because it was dominated by Tennessee Warblers. These birds peck at fruit, dispersing few seeds. This disproportionate number of Tennessee Warblers may be due to its proximity to the tree they used for perching. Tennessee Warblers almost always flew from an orange tree across the pasture into Site Three. They would often pass into Sites One or Two after foraging in Site Three, but they would rarely fly directly into these trees. There was also a very low abundance of swallowers at Site Three (n = 10), therefore the tree likely had limited dispersal.

Overall success of a given tree is due to many factors. This study has indicated that proximity to forest patches and other fruiting trees may be a determining factor for a trees' success. Crop size did not directly relate to diversity or abundance, but there was a relationship between crop size and overall success with the more successful trees having a greater number of fruits. Although dbh did not relate to success, this is not an accurate measure of crown size and the relationship between tree size and success should be further studied.

Both Jordano (1983) and Bronstein and Hoffmann (1987) found that spatial and temporal variation were important factors in determining the abundance, richness and diversity of avian dispersers at *Ficus* trees. However, neither study assessed whether abundance and diversity differed between trees with little or no spatial and temporal variation. This study found that, in the absence of these two factors, diversity, abundance and richness of birds was different between otherwise similar sites. It has been demonstrated that there are multiple factors involved in the overall success of a *F. pertusa*. However, the reasons that birds prefer foraging in certain fruiting *F. pertusa* over other nearby trees is still unclear. Future studies could address the question further, possibly doing more careful analysis of proximity to forest patches and other fruiting trees. However, the main conclusion is that several factors interact to attract dispersers to *F. pertusa* and these factors are able to change over very small scales, thus affecting the overall success of a given tree.

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Table 1. Summary of all birds seen at each F. pertusa. Total abundances of birds at each site, total abundance of each species, richness, Shannon Weiner Diversity Index and Evenness were included for comparison. Richness and total bird visits doesn't not correlate directly to diversity. See Appendix for abbreviations.

Species Name	**Site 1**	**Site 2**	**Site 3**	**Site 4**	**Total Abundance**
Tenn warbler	177	37	204	17	435
C-c robin	79	27	8	27	141
Y-t euphonia	50	10	11	1	72
B-g tanager	20	5	3	4	32
B-c motmot	12	0	1	9	22
Mtn elaenia	1	0	0	9	10
Br jay	5	1	0	3	9
H woodpecker	6	0	0	0	6
W tanager	3	0	1	2	6
B-b flycatcher	2	1	1	0	4
T warbler	3	0	0	0	3
Y-f grassquit	2	0	0	0	2
Soc flycatcher	2	0	0	0	2
Flycatcher, spp.[a]	2	0	0	0	2
B-w warbler	1	0	0	0	1
R-b grosbeak	1	0	0	0	1
Y warbler	0	0	1	0	1
B-t-g warbler	0	0	0	1	1
Bird A [a]	1	0	0	0	1
Pewee, spp.[a]	1	0	0	0	1
Warbler, spp.[a]	0	0	0	1	1
W-t robin	0	0	0	1	1
Total Abundance	368	81	230	75	754
Richness	18	6	8	11	22
H'	0.704006	0.548422	0.22575	0.792628	
Evenness	.5840424	.70477057	.24997	.72511119	
Crop Size	10,200	2,100	500	3,300	
Dbh (cm)	43.29	28.33	23.87	15.27	

[a]Species could not be determined

Table 2. Pairwise comparisons of sites. All sites were roughly similar, with Sorenson's Index ranging from 0.50 to 0.71. Five of the 7 comparisons showed significant differences diversity between the sites, showing that trees with little or no special and temporal variation show different species abundance and richness.

	Sorenson's Index	H' t-Values	Degrees of Freedom	H' p-values
Site 1 vs. Site 2	0.50	3.38	1.82E+14	<.001
Site 1 vs. Site 3	0.53	6.64	280.46	<.001
Site 1 vs. Site 4	0.55	0.50	75.75	Ns
Site 2 vs. Site 3	0.71	4.25	254.80	<.001
Site 2 vs. Site 4	0.53	1.35	81.04	Ns
Site 3 vs. Site 4	0.63	3.00	82.01	<.005
Site 1, 2, 3 vs. Site 4	0.55	7.36	227.30	<.001

Table 3. Summary of foraging behavior of birds in F. pertusa. Average weight is based on the average weight per visit, more heavily weighing the more abundant birds in the average weight per category. See Appendix for abbreviations.

Foraging Behavior	Peck	Mash	Swallow
Species Common Name	Tenn Warbler B-t-g	B-g Tanager Y-t Euohonia R-b Grosbeak W Tanager	C-c robin B-c motmot H woodpecker Soc flycatcher B-b flycatcher Mtn elaenia Br. jay Flycatcher, spp.[a]
Abundance	437	111	199
Richness	2	4	8
Average Weight (g)	8.5	20.8	84.2

[a]Species could not be determined

Table 4. Summary of foraging behavior at each site in the pasture. Site One has the highest abundance of swallowers, the most efficient dispersers, although Site Four has the highest proportion of swallowes. Both trees are likely being dispersed well. In contrast, Site Three has a high number of pecking birds, the worst dispersers, and low number of swallowing birds. Thus, it likely has limited dispersal. Site Two is being dispersed better than Site Three, due to its higher number of swallowers, but worse than Sites One and Four.

Foraging Behavior	Site One	Site Two	Site Three	Site Four	Total	Chi-Square p-value
Peck	177	37	204	18	437	
Ash	74	15	15	7	111	
Swallow	109	29	10	49	197	
Unknown	8	0	1	1	10	
Total	368	81	229	75	754	

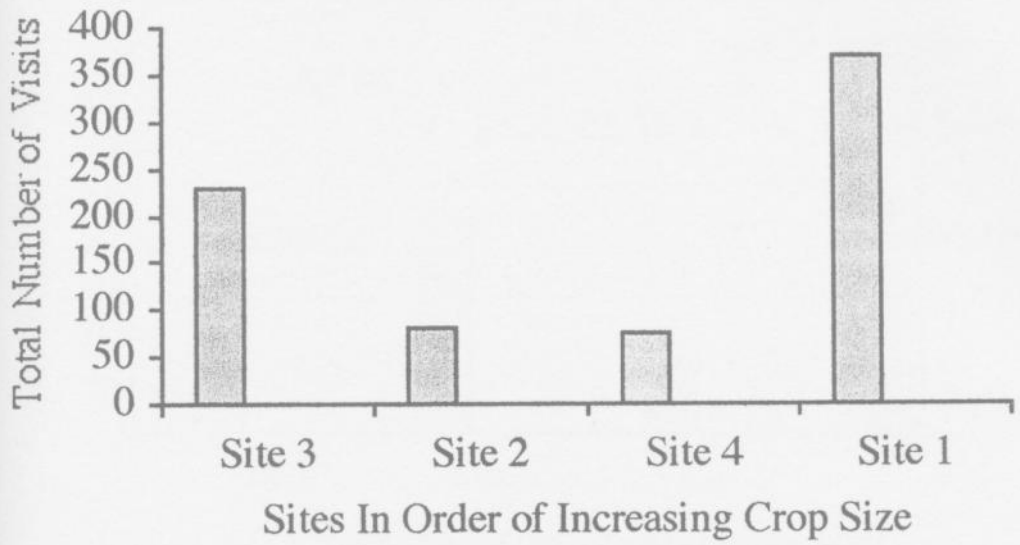

Figure 1. Crop size for each tree was 500, 2,100, 3,300 and 10,200. Although the tree with the most fruits had the highest number of visits, no clear relationship was found.

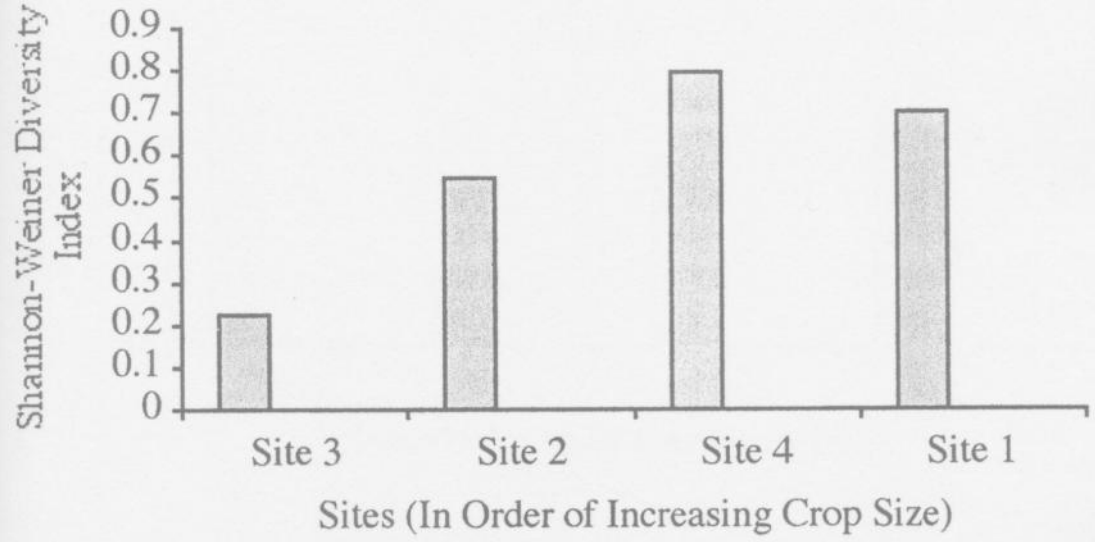

Figure 2. Crop size for each tree was 500, 2,100, 3,300 and 10,200. Although no clear relationship can be demonstrated between crop size and diversity, there is a general trend towards increasing diversity as crop size increases.

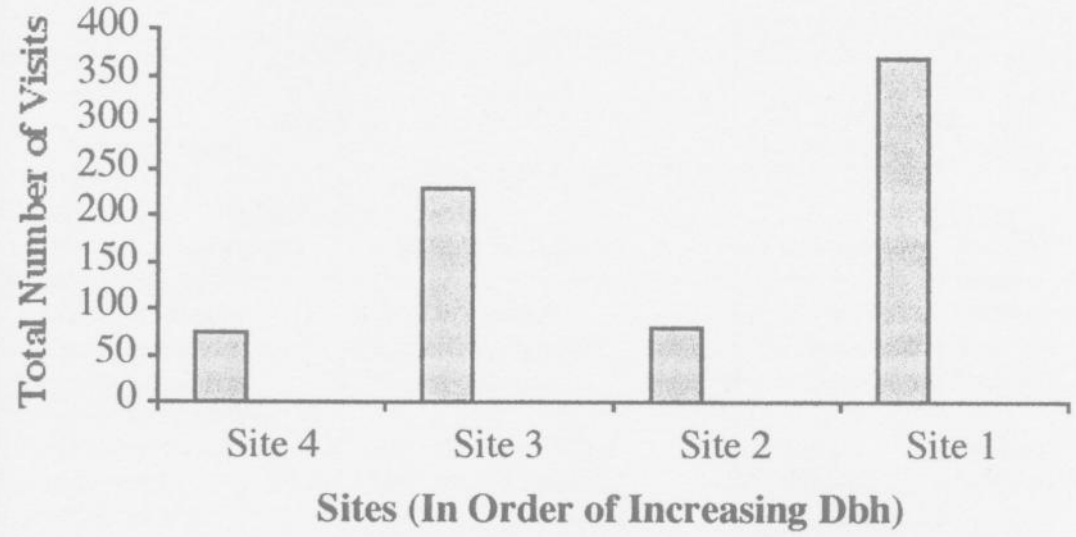

Figure 3. Dbh of each tree was 15.27, 23.87, 28.33 and 43.29 cm. No relationship was found between tree size and the Shannon-Weiner Diversity Index. In fact, the smallest tree had the highest diversity, opposite from what was expected.

Figure 4. Dbh of each tree was 15.27, 23.87, 28.33 and 43.29 cm, in order of increasing size. Small size may be a constraint, however there is no clear relationship between dbh and total number of visits.

Appendix

Scientific and common names of birds identified at *F. pertusa*, including abbreviations used in tables. Foraging behavior also included.

Scientific Name	Common Name	Abbreviation	Foraging Behavior
Family Motmotidae			
Motmotus momota	Blue Crowned Motmot	B-c motmot	Swallow
Family Picidae			
Melanerpes hoffmannii	Hoffman's Woodpecker	H woodpecker	Swallow, Glean
Family Tyrannidae			
Myiozetetes similis	Social Flycatcher	Soc flycatcher	Swallow
Megarhynchus pitangua	Boat Billed Flycatcher	b-b flycatcher	Swallow
Elaenia franzii	Mountain Elaenia	Mtn elaenia	Swallow
Family Muscicapidae			
Turdus assimilis	White Throated Robin	W-t robin	Swallow
Turdus grayi	Clay Colored Robin	C-c robin	Swallow
Family Corvidae			
Psilorhinus morio	Brown Jay	Br jay	Swallow
Family Praulidae			
Vermivora peregrine	Tennessee Warbler	Tenn warbler	Peck
Mniotilta varia	Black and White Warbler	B-w warbler	Glean
Dendroica petechia	Yellow Warbler	Y warbler	Perch
Dendroica townsendi	Townsend's Warbler	T warbler	Perch
Dendroica virens	Black Throated Green Warbler	B-t-g warbler	Peck, Glean
Family Thraupidae			
Euphonia hirundinacea	Yellow Throated Euphonia	Y-t euphonia	Mash
Thraupis episcopus	Blue Gray Tanager	B-g tanager	Mash
Piranga ludoviciana	Western Tanager	W tanager	Mash
Family Emberizidae			
Pheuciticus ludovicianus	Rose Breasted Grosbeak	R-b grosbeak	Mash
Tiaris olivacea	Yellow Faced Grassquit	Y-f grassquit	Perch
Family Ramphastidae[a]			
Aulacorhybchus prasinus	Emerald Toucanet	Em toucanet	
Ramphastos sulfuratus	Keel Billed Touca	K-b toucan	
Family Icteridae[a]			
Icterus g. galbula	Northern Oriole	N oriole	
Psarocolius montezuma	Montezuma Oropendula	M oropendula	

[a]Species seen foraging on F. pertusa outside of the observation period.