CLOUDBRIDGE
NATURE RESERVE

Surveys of Mixed Species Feeding Flocks in Cloudbridge Nature Reserve, Costa Rica: A Progress Report.

Jonathan Slifkin

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A Common Chlorospingus (*Chlorospingus flavopectus*), the most commonly observed bird in Cloudbridge Nature Reserve and a typical mixed species feeding flock leader. Photograph © Jonathan Slifkin.

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1 ABSTRACT

Mixed species avian feeding flocks, are less studied in montane habitats and in secondary forest. Mixed flocks were studied at Cloudbridge Nature Reserve, in the Costa Rican cloud forest, in naturally regenerated and replanted forest as well as old growth, from February to March 2019, and April to June 2019. This progress report summarizes the survey methods and results from the second round of surveys. Cumulative frequency of species within mixed flocks, flocking propensity of different species, family composition of mixed flocks, flock diversity and size, nucleus and attendant species, flock distribution across forest types, and flock composition over the course of the year were analyzed. Most results agree with prior research findings in similar habitats, such as the dominance of the genus *Chlorospingus* and typical presence of certain Parulids and Furnariids in mixed flocks, or the typically smaller size and diversity of mixed flocks at higher elevations. Other results, such as a lack of preference between forest types by mixed flocks, contrast to prior findings and require further investigation. The continuation of mixed species feeding flocks surveys at Cloudbridge should be continued, as they will yield more comprehensive and significant results over time.

2 INTRODUCTION

Mixed species avian feeding flocks, comprised of individuals of multiple bird species moving and foraging together, are a phenomenon familiar to ornithologists and birders in terrestrial habitats almost everywhere in the world. As a perennial research focus, mixed flocks have been shown to vary greatly across different habitats, localities, and regions of the world in their size, structure, species diversity, family composition, and adaptive and ecological functions (Sridhar et al. 2009; Kajiki et al. 2018). Still, the bulk of our knowledge of mixed flocks (including in the Neotropics) has come from lowland forest habitats (Kajiki et al. 2018). Information on mixed flocks in montane habitats remains less developed, despite the well-known ecological and ornithological significance of such habitats as the Costa Rican montane cloud-forest (Soane 2019; Kajiki et al. 2018). Furthermore, the implications for mixed flocks of ever-increasing deforestation and fragmentation of all forest habitats, and the role that mixed flocks might play in understanding habitat quality and directing conservation attention, have only recently become research priorities (Kajiki et al. 2018). In light of these knowledge shortfalls, surveys of mixed species feeding flocks were developed and conducted by Isabel Soane and Jeffrey Roth, from February 12 to March 30, 2019, at Cloudbridge Nature Reserve, a private nature reserve on the Pacific slope of the Talamanca Mountains in southwestern Costa Rica. Surveys were conducted along transects of naturally regenerated forest, actively replanted forest, and old-growth forest. A report was produced laying out their preliminary results (Soane 2019).

This project was conceived as a long-term data collection effort. As such, after Roth's and Soane's departures from Cloudbridge, I took over responsibility for the project and continued the mixed feeding flocks surveys following their protocols, from April 22 to June 19, 2019. This progress report provides a detailed description of the survey protocols used and an overview of the data collected from my surveys, especially for use by those who will (ideally) continue this project after me. Data regarding cumulative frequency of species within mixed flocks, flocking propensity of different species, family composition of mixed flocks, flock diversity and size, nucleus and attendant species, and flock distribution across forest types are presented and discussed, with an eye to the ways in which these data may support and inform future research into mixed species feeding flocks at Cloudbridge and in cloud-forest habitats.

3 SURVEY LOCATIONS, METHODS, & MATERIALS

Soane (2019) provides a description of Cloudbridge Nature Reserve as the study area for the mixed feeding flock surveys, including its climate, elevation, terrain, and successional forest types.

The following survey protocol follows those developed and used by Soane, but are described in further detail and with a few potential modifications. Surveys were conducted along four different circuits, each in two different directions (forwards and backwards), for a total of eight survey routes. One circuit (Principal/Río/Heliconia, or RIO) begins at the base of the Principal Trail and continues along the Principal Trail to the entrance to the Río Trail, then follows the entire Río Trail to its exit at the Mirador del Valle, and then takes the Heliconia Trail down and finishes at its base. Another circuit (Jilguero/Gavilán, or JG) takes the Jilguero Trail up to its junction with the Gavilán Trail and then takes the Gavilán Trail down finishing at its junction with the Heliconia Trail. A third circuit (Montaña/Chirripó, or MON) takes the Montaña Trail up to the Chirripó Trail and then continues down the Chirripó Trail until it meets the access to the Jilguero Trail, where it finishes. The final circuit (Don Victor/Vulture Rock, or DV) begins at the base of the Don Victor Trail and continues up the Don Victor Trail and past the junction with the Vulture Rock Trail, along the Catarata Victor Trail to its marked end (just before it crosses the river to join Los Quetzales), and then, having returned to the junction with the Vulture Rock Trail (which return is not included as part of the survey), continues up the Vulture Rock Trail to Vulture Rock itself, where it finishes. See Figure 1.

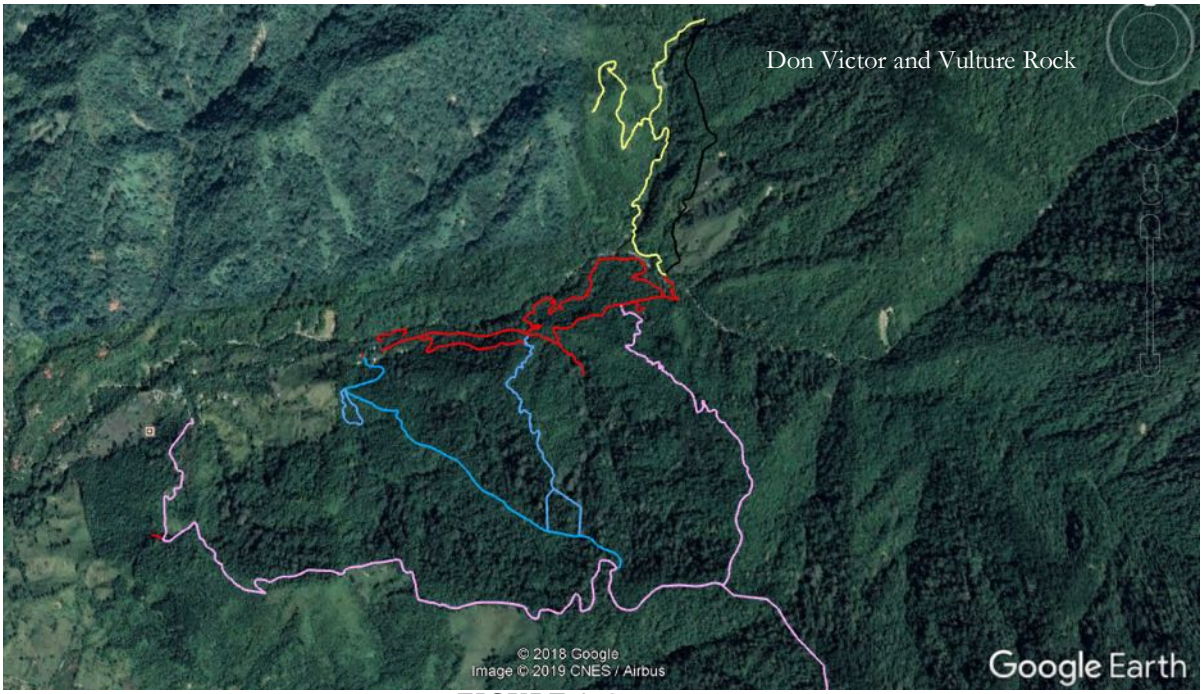

FIGURE 1: Survey Routes.

All of these circuits are marked along the way with 50-meter interval markers specifically for use in the mixed feeding flock surveys, which are either blue or orange posts in the ground or pink, orange, and/or black-and-yellow flagging tapes tied to a branch that typically read "MSF" or "MAM"[1] followed by the meter number and occasionally also by the abbreviation for the circuit (see Appendix A). Sometimes these markers have been lost, have fallen off, or have been removed by hikers and may need replacing from time to time.

A survey was conducted along one of these circuits on each survey-day, starting the circuit at 6:00 am and aiming to finish around 9:00 am, which corresponded to a pace of about 3 minutes for each 50-meter interval. As a matter of course, in each 8-survey-day period, a survey was conducted along each circuit once forwards and once backwards (i.e., following the circuit in the opposite direction as described, beginning at the end of the circuit at 6:00 am, etc.), otherwise in no necessary order. The Don Victor/Vulture Rock circuit became inaccessible following a severe rainstorm on May 22, 2019, and thereafter only the other three circuits (six survey routes) were surveyed.

Surveys proceeded as follows. At the beginning of the circuit the time (6:00 am) was recorded along with the rain, wind, and cloud conditions (see Appendix B). The same information (time and rain, wind, and cloud conditions) was also recorded at each change in trail along the circuit (e.g., when exiting the Montaña Trail and entering the Chirripó Trail along the Montaña/Chirripó circuit) as well as at the mid-point of the Principal Trail (at the Mirador del Valle), simply to serve as convenient subdivisions, and finally at the end of the survey. Two different kinds of information about the birds encountered during the survey were recorded. Firstly, a running tally was kept of every bird species seen that was *not* in a mixed flock, and the number thereof, along each of these subdivisions. For example, if six Slate-throated Redstarts (*Myioborus miniatus*) were seen along the Montaña/Chirripó circuit, four along the Montaña Trail and another two along the Chirripó Trail, then "Slate-throated Redstart" would be listed under "Montaña Trail" with a tally of four, and would also be listed under "Chirripó Trail" with a tally of two. These records provided background information about species occurrence along the survey routes. Secondly, a separate record was kept of each mixed species feeding flock encountered along the circuit. If and when a mixed feeding flock was encountered, every species and the number thereof that was present in the flock was recorded, along with the time at which the flock was encountered and the meter number of the 50-meter interval marker closest to the point at which the flock was encountered. All reasonable efforts were made to stay with the flock if and as it moved in order to record every species participating in it over time. Birds were observed using a Canon 5DS camera with a 100–400mm lens,[2] and information was recorded in the field in a notebook.

What, then, is a mixed species feeding flock? For the purposes of these surveys, a mixed feeding flock was technically defined as at least one individual each of at least two different species, moving and foraging together in the same general direction. Thus, for example, one Common Chlorospingus (*Chlorospingus flavopectus*) and one Slate-throated Redstart moving and foraging together would count as a mixed feeding flock, whereas a flock of six Common Chlorospinguses moving and feeding together unaccompanied by an individual of another species would not. Multiple species aggregating at the same stationary resource, such as a flowering or fruiting tree, also would not count as a mixed feeding flock, as these birds would not be moving together in a certain direction. This exclusion makes

1. Whereas MSF stands for "mixed species flocks," MAM stands for "mammals." These markers were for use in mammal surveys which are no longer conducted, but they are located and numbered the same as for the mixed feeding flocks surveys.

2. Soane (2019) used a pair of binoculars rather than a camera for her surveys, which is presumably a more standard tool for these purposes. Both have their advantages and disadvantages as tools for bird surveying.

sense insofar as the focus of the study is on interspecific flocking behavior, not simply coincidental aggregation (see Sridhar et al. 2009). To be sure, it was often difficult to make a judgement in the field as to whether a particular bird was really moving and foraging in the same general direction as another, or if the two simply happened to be crossing paths coincidentally, although observing the flock (or potential flock) for as long as possible helped in such situations. Finally, based on a widely-accepted distinction between "nucleus," "core," or "leader" species which are highly vocal and lead the movement of a flock, and "attendant" or "follower" species which follow the nucleus species (Rand 1954, cited in Soane 2019; Sridhar et al. 2009), a determination was made wherever possible as to which species was serving as the nucleus species in each flock encountered.

4 RESULTS

Thirty surveys were conducted from April 22 to June 19, 2019, during which 31 mixed species feeding flocks composed cumulatively of 189 individuals of 32 different bird species were encountered.[3] As noted by Soane (2019), the sample size of these data remains small, a flaw that characterizes a great deal of research into mixed flocks (Sridhar et al. 2009), and any results must be treated as preliminary. As mentioned, this project was conceived as a long-term data collection effort and ought to be continued so that it may eventually yield more significant and informative results. Nevertheless, preliminary results are presented herein regarding certain salient aspects of the data, *viz.*, cumulative frequency of species within mixed flocks, flocking propensity of different species, family composition of mixed flocks, nucleus and attendant species, flock diversity and size, and flock distribution across forest types.

4.1 SPECIES FREQUENCY

Figure 2 presents a cumulative frequency count of each of the 32 species observed within mixed flocks over all 30 surveys. By far the most commonly observed species was the Common Chlorospingus, of which there were 50 observations within mixed flocks, comprising 26.46%, more than a quarter, of all birds observed within mixed flocks. After the Common Chlorospingus, the most frequently encountered species were the Red-headed Barbet (*Eubucco bourcierii*), the Silver-throated Tanager (*Tangara icterocephala*), and the Slate-throated Redstart, each with 13 records within mixed flocks. Obviously, many species were recorded only a few times, or only once in mixed flocks. Furthermore, not every species observed during the surveys was recorded within mixed flocks; in total, 108 different bird species were recorded during the surveys, of which the 32 bird species recorded within mixed flocks comprises only 29.63%.

3. This does not include—and this report does not include any data from—the May 22 survey which was aborted due to the onset of heavy rain. Incidentally, this was the same rainstorm that rendered the Don Victor/Vulture Rock circuit inaccessible (see above).

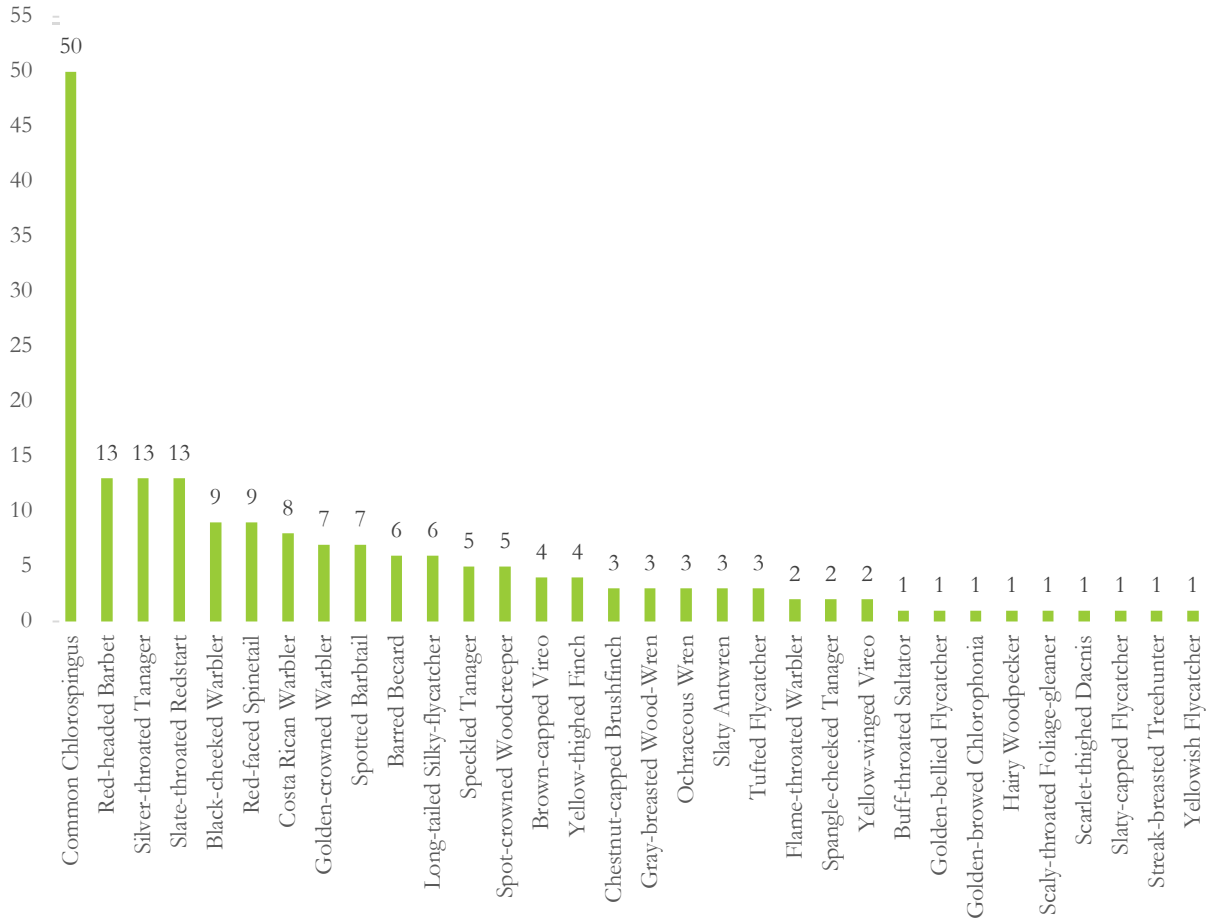

FIGURE 2: Species Frequencies within Mixed Flocks.

4.2 FLOCKING PROPENSITY

Another way to gauge the relationship between mixed species flocks and individual species, aside from the bare cumulative frequency of each species observed within mixed flocks, is to calculate the "flocking propensity" of each species. This is calculated by summing the total number of observations of a given species during surveys and determining what percentage of those observations occurred in mixed flocks (Sridhar et al. 2009). The flocking propensity of a species thus aims to reflect the probability that said species will participate in mixed flocks. Soane (2019) did not calculate or discuss flocking propensities, perhaps due to the tiny sample sizes involved; however, this metric will presumably come to be of greater use if and as this project continues and more data is collected. Table 1 presents the flocking propensities of all 32 species observed within mixed flocks during my surveys, ordered from highest to lowest propensity.

Some of these calculated flocking propensities are presumably of little interest, especially the very high percentages resulting from extremely small sample sizes, although it is certainly possible that such species, such as Barred Becard (*Pachyramphus versicolor*) (75.0%), are indeed far easier to observe in

mixed flocks than outside mixed flocks. Of greater significance may be the flocking propensities of the species most frequently encountered in mixed flocks, for which more data is available. For instance, although Common Chlorospingus was by far the most frequently encountered species in the mixed flocks, its flocking propensity (29.8%) is lower than that of one of the second most frequently encountered species, the Red-headed Barbet (43.3%), because it was also observed so frequently outside mixed flocks. Meanwhile, the flocking propensities of the other two second most frequently encountered species, Silver-throated Tanager (24.1%) and Slate-throated Redstart (15.9%), are lower still, and indeed these two species were also frequently encountered outside mixed flocks, the Silver-throated Tanager often in single-species flocks and the Slate-throated Redstart often in pairs.

TABLE 1: Flocking Propensities.

Species	Number of observations outside mixed flocks	Number of observations in mixed flocks	Flocking propensity
Flame-throated Warbler	0	2	100.0%
Barred Becard	2	6	75.0%
Tufted Flycatcher	1	3	75.0%
Yellow-winged Vireo	2	2	50.0%
Red-faced Spinetail	11	9	45.0%
Costa Rican Warbler	10	8	44.4%
Ochraceous Wren	4	3	42.9%
Red-headed Barbet	18	13	41.9%
Black-cheeked Warbler	13	9	40.9%
Slaty Antwren	5	3	37.5%
Slaty-capped Flycatcher	2	1	33.3%
Spangle-cheeked Tanager	4	2	33.3%
Speckled Tanager	11	5	31.3%
Common Chlorospingus	118	50	29.8%
Spotted Barbtail	20	7	25.9%
Golden-bellied Flycatcher	3	1	24.0%
Golden-crowned Warbler	22	7	24.1%
Silver-throated Tanager	41	13	24.1%
Spot-crowned Woodcreeper	18	5	21.7%
Long-tailed Silky-Flycatcher	22	6	21.4%
Golden-browed Chlorophonia	4	1	20.0%
Scaly-throated Foliage-gleaner	4	1	20.0%
Yellow-thighed Finch	16	4	20.0%
Brown-capped Vireo	19	4	17.4%
Hairy Woodpecker	5	1	16.7%
Slate-throated Redstart	71	13	15.5%
Buff-throated Saltator	6	1	14.3%
Chestnut-capped Brushfinch	24	3	11.1%
Yellowish Flycatcher	8	1	11.1%
Streak-breasted Treehunter	9	1	10.0%
Gray-breasted Wood-Wren	30	3	9.1%
Scarlet-thighed Dacnis	11	1	8.3%

4.3 FAMILY COMPOSITION

Figure 3 presents the percentage of avian families present in all the mixed flocks recorded. New World Sparrows (*Emberizidae*) comprised the largest share, accounting for approximately 30 percent of all the birds recorded within the flocks. Given that only two species of emberizid other than Common Chlorospingus were recorded within the flocks—Yellow-thighed Finch (*Pselliophorus tibialis*) with 4 records and Chestnut-capped Brushfinch (*Arremon brunneinucha*) with 3—this result for the most part simply reflects the overwhelming abundance of the Common Chlorospingus. Similarly, the relatively large percentage comprised by the New World Barbets (*Capitonidae*) simply reflects the relatively high frequency of the Red-headed Barbet, the only representative of its family at Cloudbridge, and indeed in all of Costa Rica, within mixed flocks.

By contrast, the second most represented family, the New World Warblers (*Parulidae*), included a number of fairly well-represented species, notably Slate-throated Redstart, Black-cheeked Warbler (*Basileuterus melanogenys*), Costa Rican Warbler (*Basileuterus melanotis*), and Golden-crowned Warbler (*Basileuterus culicivorus*) (see Table 1). Ovenbirds (*Furnariidae*) also included a few fairly well-represented species such as Red-faced Spinetail (*Cranioleuca erythrops*), Spotted Barbtail (*Premnoplex brunnescens*), and Spot-crowned Woodcreeper (*Lepidocolaptes affinis*), while Tanagers (*Thraupidae*) were represented largely by Silver-throated Tanagers plus a range of less frequent species. A range of families were represented in the mixed flocks by only a few individuals, in some cases of only one species, such as the Barred Becard in *Tityridae* (3.17%) or the Slaty Antwren (*Myrmotherula schisticolor)* in *Thamnophilidae* (1.59%). Finally, there were some avian families that, although well represented both by species diversity and by number of individual birds observed outside of mixed flocks, were never once recorded within a mixed flock, notably *Turdidae* (Thrushes) and, of course, *Trochilidae* (Hummingbirds), among others.

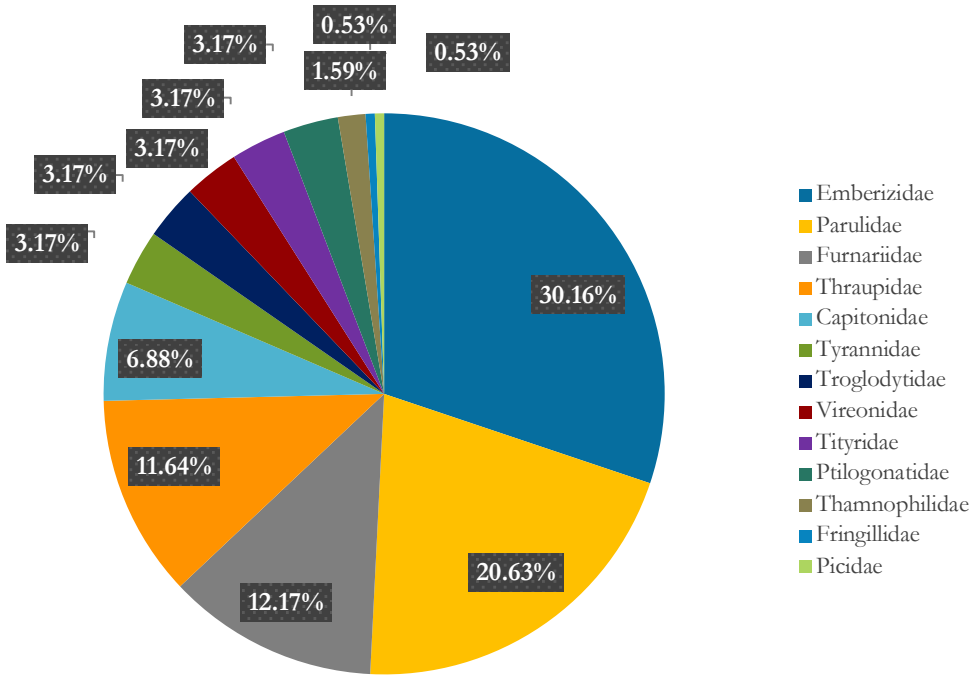

FIGURE 3: Family Composition of Mixed Flocks.

4.4 NUCLEUS AND ATTENDANT SPECIES

As described above, the nucleus species of a mixed species flock is a highly vocal participant in the flock that leads the flock's movement. A nucleus species was ascertained for 16 of the total 31 encountered mixed flocks. For the other 15 flocks, the nucleus species was not ascertained, due to the presence of multiple highly vocal species, or no highly vocal species, in the flock and/or the difficulty of determining which species in particular was at the forefront of the flock's movement (see Section 5.1). Only four species were recorded as nucleus species: Common Chlorospingus in 11 flocks, Black-cheeked Warbler in 3 flocks, Golden-crowned Warbler in 1 flocks, and Flame-throated Warbler (*Oreothlypis gutturalis*) in 1 flock. When identified, the nucleus species was present in its mixed flock either in pairs or in small groups of 3 or 4, except for one occasion on which a lone Common Chlorospingus was identified as the nucleus species in a flock. Other than Flame-throated Warbler, which was only ever recorded in one flock, the Common Chlorospingus, Black-cheeked Warbler, and Golden-crowned Warbler were all also recorded as present within mixed flocks for which they were not recorded as the nucleus species; moreover, both Black-cheeked Warbler and Golden-crowned Warbler were recorded within mixed flocks in which Common Chlorospingus was also present. Presumably, then, the same species may serve as a nucleus species on one flock, but as an attendant species in another. All the other species present in a flock for which a nucleus species was ascertained may be considered attendant species in that flock.

4.5 FLOCK DIVERSITY AND SIZE

Figure 4 summarizes the species diversity of the mixed flocks encountered, distributing the 31 flocks according to the number of species recorded within them. Most flocks were rather limited in diversity, being composed of between 2 and 5 different species, with 3 species being the mode. The mean flock diversity was 3.49 species. However, two flocks were dramatically more diverse than the rest, containing 11 and 12 species each. Interestingly, although these two flocks contained a number of different species (see Appendix C), they were seen within a few days and within 100m of each other (the 12-species flock on June 5 at RIO 1450m and the 11-species flock on June 8 at RIO 1350m).

Figure 5 summarizes the size of the mixed flocks by individual birds, distributing the 31 flocks according to the number of individual birds recorded within them. Most flocks were also fairly small, containing between 3 and 8 individual birds, with 5 being the mode. The mean flock size was 6.10 individual birds. Unsurprisingly, the two notable outliers, a flock containing 24 individuals and a flock containing 18 individuals, are the very same as the two most diverse flocks mentioned above.

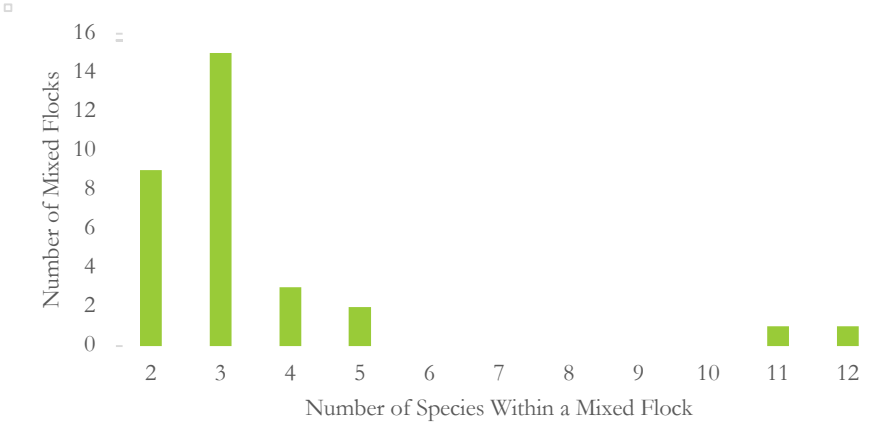

FIGURE 4: Mixed Flocks by Species Diversity

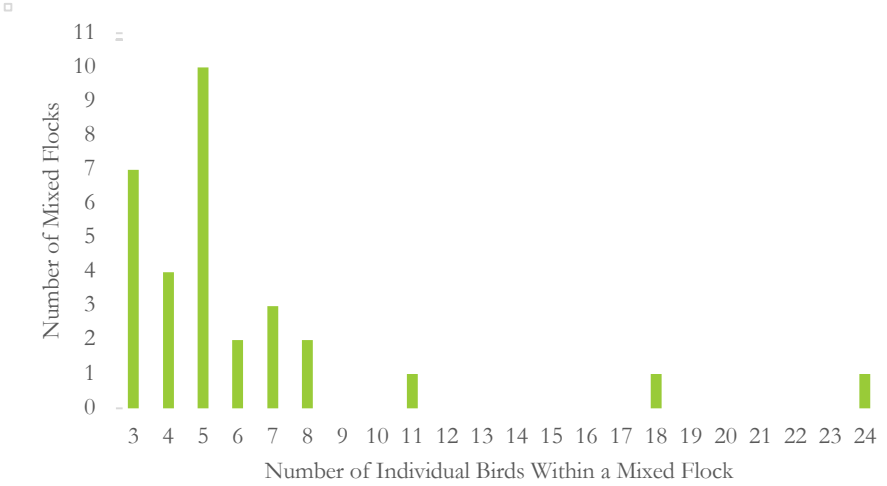

FIGURE 5: Mixed Flocks by Size.

4.6 FOREST TYPE DISTRIBUTION

Of the 31 total mixed flocks encountered, 10 were encountered in planted areas, 13 in areas of natural regeneration younger than 30 years, 4 in areas of natural regeneration older than 30 years, and 4 in old growth forest. In order to test whether mixed flocks displayed any preference between any of these forest types, the percentage of the entire distance surveyed in each forest type was compared to the percentage of all encountered mixed flocks that were encountered in each forest type. The null hypothesis was that mixed flocks would display no preference between forest types, in which situation we would expect to see the mixed flocks distributed evenly along the survey distance without regard to the forest types, and thus the percentage of mixed flocks encountered in one forest type would simply be the same as the percentage of the total survey distance taken up by that forest type. See Soane 2019.

For the purposes of these calculations, the Don Victor/Vulture Rock circuit (consisting of 2400m of natural regeneration younger than 30 years) was disregarded due to the cessation of surveys along that circuit after May 22 (see above), and so the three mixed flocks cumulatively encountered along that circuit while it was still being surveyed were likewise disregarded. Accordingly, the remaining data consists of 10 mixed flocks encountered in planted areas, 10 in areas of natural regeneration younger than 30 years, 4 in areas of natural regeneration older than 30 years, and 4 in old growth forest. See Table 2.

When standardized to the number of flocks seen per 1000 m of habitat surveyed, the results were fairly similar between habitat types, ranging from 3.1 in natural regeneration under 30 years and old growth, to 4.7 in natural regeneration older than 30 years. Based on these results, the null hypothesis appears not to be rejected, and the flocks do not appear to display a preference for certain forest types over others. A Chi-squared test confirmed this impression, yielding a P-value of 0.909, indicating no statistically significant deviation from the null hypothesis.

TABLE 2: Forest Type Preference

Forest Type	Habitat		Flocks	
	Cumulative distance along all survey routes*	**Percentage of total survey distance***	**Number of flocks encountered***	**N / 1000 m of habitat**
Planted	2850m	**34.76%**	10	**3.5**
Natural regeneration younger than 30 years	3200m	**39.02%**	10	**3.1**
Natural regeneration older than 30 years	850m	**10.37%**	4	**4.7**
Old growth	1300m	**15.85%**	4	**3.1**

*Not including values or data from Don Victor/Vulture Rock.

5 DISCUSSION & CONCLUSIONS

5.1 FLOCK COMPOSITION

The abundance and conspicuousness of the Common Chlorospingus within mixed species feeding flocks are well-known (Buskirk et al. 1972; Hilty 2019; Soane 2019) and they stand out prominently in the results from my surveys as well. The Common Chlorospingus was also by far the most frequently recorded nucleus species, in keeping with previous research findings designating this species as the typical, or even the only, nucleus species in mixed flocks where it occurs (Buskirk et al. 1972; Buskirk 1976). Indeed, the genus *Chlorospingus* has been found to include the main nucleus species and most frequent participants in mixed flocks in other Neotropical montane habitats (Soane 2019). At the same time, of course, and as corroborated by its calculated flocking propensity of 29.76%, the Common

Chlorospingus is a common and conspicuous species in general and can often be found in small intraspecific groups as well.

Most of the species recorded in mixed flocks during my surveys are either predominantly insectivorous or both insectivorous and frugivorous. Common Chlorospingus is known to forage by actively gleaning insects, taking nectar from flowers, and eating small fruits whole as it moves through the forest (Hilty 2019). Red-headed Barbet, likewise, is known to feed upon a variety of fruits as well as a variety of insects and other arthropods; as such, it is known to gather intraspecifically at fruiting trees, but also to join mixed species feeding flocks (Short and Horne 2019). Slate-throated Redstart, on the other hand, feeds strictly on insects and other arthropods, foraging actively by gleaning and flycatching; it has also been noted as frequently joining mixed species feeding flocks (Curson and de Juana 2019). These diets and foraging strategies are compatible with the relatively constant, continuous pace taken by mixed feeding flocks (Buskirk 1976). Other diets and foraging strategies are less compatible, which helps to explain the absence of certain species and families from the mixed flocks. This included, most obviously, the near-totally nectivorous *Trochilidae* (Hummingbirds), but also, for example, some species from *Tyrannidae* (New World Flycatchers), representing only 3.17% of the species encountered within mixed flocks, which often forage by sallying or hover-gleaning from a stationary position over a longer period of time. In fact, it is important to note that the Yellowish Flycatcher (*Empidonax flavescens*), which forages mostly for arthropods by sallying and hover-gleaning, has been specifically noted as *not* participating in mixed species flocks; as such, it is possible that my single record of a Yellowish Flycatcher in a mixed flock (see above) was based on a coincidental co-occurrence between the flycatcher and a flock passing through (Farnsworth et al. 2019).

In general, then, much of my survey results comported with prior research into mixed flocks in similar habitats; for example, Buskirk's research into mixed flocks in tropical highland Panama (which shares a number of ecological features including endemic bird species with tropical highland Costa Rica), found Common Chlorospingus to be the most common mixed flock participant, and listed such familiar species as Red-headed Barbet, Barred Becard, Red-faced Spinetail, Black-cheeked Warbler Slate-throated Redstart, Spot-crowned Woodcreeper, and Silver-throated Tanager as flock participants (Buskirk et al.1972). There were a few notable cases, however, in which the relative abundance of a species within mixed flocks differed between my surveys and those conducted in the months prior by Soane. In Soane's surveys, the second most frequently encountered species in mixed flocks was the Golden-crowned Warbler (22 records), followed by the Costa Rican Warbler and Yellow-thighed Finch (14 records each). Furthermore, Soane found that all three of these species served as nucleus species in mixed flocks, and that one of them or the Common Chlorospingus served as the nucleus species in every flock she encountered (Soane 2019). By contrast, although all three of these species were represented in the mixed flocks encountered during my surveys, they were not as relatively frequent as in Soane's surveys, and none of them was ever recorded as a nucleus species in a flock. Conversely, in my surveys the second most frequently encountered species in mixed flocks were Red-headed Barbet, Silver-throated Tanager, and Slate-throated Redstart, whereas in Soane's surveys, the Red-headed Barbet and Silver-throated Tanager were not recorded especially frequently (6 records and 5 records respectively) and, most notably, the Slate-throated Redstart was never once recorded within a mixed flock. This discrepancy deserves further investigation, although it is conceivable that it is partially explicable by breeding timing, since Slate-throated Redstarts are known frequently to join mixed flocks *outside* of breeding season (Curson and de Juana 2019).

Indeed, most of my surveys took place in what can be thought of as a general breeding season. To be sure, different species breed at different times of year and breeding can often occur over a wide range of time even within one species in one area. Climate change may also be affecting breeding timing in unpredictable ways. Nonetheless, typically speaking, nesting occurs in southern Costa Rica in the first three months of the wet season, traditionally April through June (Skutch 1950). The fact that my surveys took place over the course of the breeding season likely affected my results in two notable ways. Firstly, nesting birds tend to be less vocal and less conspicuous overall and, as mentioned in the case of the Slate-throated Redstart, may tend to participate in mixed flocks less than usual. It is possible, therefore, that my results underestimate the usual size or diversity of mixed species flocks or the flocking propensity of certain species. Secondly, many species in the Costa Rican highlands disperse to lower altitudes post-breeding. This may explain why certain species that were previously recorded only at the highest surveyed elevations (on the Chirripó or Vulture Rock Trails), or not at all, were first recorded or began to be recorded at lower elevations, including in mixed flocks, only in the last few weeks of my surveys: these species are Long-tailed Silky-Flycatcher (*Ptiliogonys caudatus*), Flame-throated Warbler, Yellow-winged Vireo (*Vireo carmioli*), Hairy Woodpecker (*Dryobates villosus*), Tufted Flycatcher (*Mitrephanes phaeocercus*), and Spangle-cheeked Tanager (*Tangara dowii*). For example, the Yellow-winged Vireo (which is noted as "sometimes" joining mixed flocks) is typically found above 1900m in Costa Rica but moves downslope as low as 1500m during the wet season (Brewer 2019). Of course, another difference between the species composition of mixed flocks between my surveys and Soane's is that Soane recorded a number of migrant species, such as Golden-winged Warbler (*Vermivora chrysoptera*), Tennessee Warbler (*Oreothlypis peregrina*), Wilson's Warbler (*Cardellina pusilla*), and Philadelphia Vireo (*Vireo philadelphicus*), within mixed flocks (Soane 2019), whereas these species had departed for their breeding grounds by the time my surveys began. In these, and presumably other, ways the time of year affects the species composition of mixed flocks.

Overall, as mentioned before, the limited amount of data collected from my surveys presented a variety of obstacles to further analysis. However, if and as mixed species feeding flocks surveys continue at Cloudbridge, these obstacles will be more easily overcome: observations from all times of year over multiple years will give a more complete picture of species composition from season to season; calculated flocking propensities, especially, will be of much greater use when they are based on larger numbers of observations of each species; and data aggregated over all conducted surveys will provide more significant and informative results about all aspects of flock composition.

Instead, two deeper difficulties with these surveys are worthy of mention. Firstly, the least successful component of data collection was the ascertainment of nucleus species. As mentioned, it was often difficult to determine, based on the two criteria of a highly vocal species and the species leading the movement of the flock, which species was serving as the nucleus species in any given flock. Often, especially in larger flocks, many species were highly vocal simultaneously, and it was often impractical to maintain contact with the flock for long enough to tell which species was typically at the forefront of the flock's movement, or which species the other species appeared to follow. Moreover, it was not always clear that the most vocal species was also the one leading the movement of the flock.

In fact, despite the widespread acceptance of the distinction between nucleus and attendant species, this distinction has received multiple different formulations in the literature, involving foraging behavior, territorial behavior, and vocalization functions as well as physical direction of a flock's

movement; Buskirk, for example, criticizes Moynihan's original definition of a nucleus species as that "whose behavior contributes appreciably to stimulate the formation and/or maintain the cohesion of mixed flocks" as overly dependent on "subjective interpretation" (Buskirk et al. 1972). Successful research into mixed flocks often involves a more complex and specific categorization of species roles within mixed flocks, involving observations of territorial behavior, amount of time spent and amount of distance traveled within a particular flock, etc. Furthermore, successful research into the roles of different species within mixed flocks often demands more intensive and sophisticated methods to ascertain each role, including large-scale color-banding of individual birds and maintaining contact with particular flocks over long periods of time, even over the course of an entire day (Buskirk et al. 1972; Munn and Terborgh 1979). Perhaps, for the purposes of future surveys at Cloudbridge, a larger set of simpler objective observations as to movements and vocalizations could be designated, in place of a directive simply to identify one species as "nucleus" and the rest as "attendant."

Secondly, one aspect of mixed feeding flocks in montane habitats, and indeed one of the reasons that research into mixed feeding flocks has historically been biased towards lowland habitats, is the fact that mixed flocks appear to be more stable over time and space and more regularly dominated by certain species or groups of species in lowland habitats than in montane habitats. Mixed flocks also tend to be smaller in the number of participating individuals at higher elevations (Kajiki et al. 2018). This means, for example, that mixed flocks may be harder to encounter and harder to recognize given their relative lack of cohesion at higher elevations. The situation in certain tropical lowlands, whereby long periods of few bird observations are punctuated by the appearance of large noisy unequivocal mixed flocks moving clearly in a certain direction, usually numbering in the dozens and sometimes in the hundreds of individuals (Kajiki et al. 2018), is far less clear-cut in montane habitats. Of course, this is all the more reason that long-term data collection on mixed flocks in montane habitats is an important area of research.

5.2 FOREST TYPE PREFERENCE

Aside from a general knowledge shortfall regarding mixed species feeding flocks in montane forest habitats, the other major impetus behind the introduction of mixed species feeding flocks surveys at Cloudbridge Nature Reserve was the opportunity to gauge potential preferences by mixed species flocks between different successional forest types and different types of secondary forest (naturally regenerated versus actively replanted). My data, which failed to show any strong mixed feeding flock preference for one such forest type over another, stand in contrast to Soane's findings on this point, which revealed "a distinct preference toward old growth with generally fewer observations in the planted sections" (Soane 2019). Prior research in the Neotropics has certainly shown that better preserved forest habitats tend to contain more, larger, and more diverse mixed species feeding flocks, which are negatively affected by deforestation and habitat fragmentation, and has suggested that mixed flocks may be useful for conservation studies as an indicator of habitat quality (Kajiki et al. 2018). However, this research has focused more on the effects of deforestation than on the effects of reforestation, i.e., the ways in which mixed flocks might interact with secondary as opposed to old-growth forest, or how effectively different types of reforestation efforts may support mixed flocks. Once again, more surveys conducted over time will yield more informative data on these points.

6 CONCLUSION

Much of the results of my surveys, preliminary though they may be, tended to confirm the findings of prior research on mixed species feeding flocks in montane habitats and, specifically, in the montane cloud forest of Costa Rica (and Panama), from the high frequency of the Common Chlorospingus in mixed flocks to the relatively small size and diversity of most mixed flocks in montane habitats. My results regarding nucleus and attendant species were limited in their informativeness by the difficulty of assessing such species roles during visual surveys, and future surveys may benefit from recording a more detailed, less subjective set of observations as to the movements and vocalizations of species participating in mixed flocks. My results regarding forest type preferences by mixed flocks, which failed to demonstrate any such preferences and thus stand in contrast to Soane's results from the months prior, are obviously deserving of further investigation. Finally, likely changes in mixed flock composition over the course of the year, some of which are already detectable in the results from my and Soane's surveys, suggest that surveys continued over the course of the year would yield a more comprehensive picture of mixed species feeding flocks at Cloudbridge.

In sum, then, my most important recommendation for the future of this project is simply that the mixed species feeding flocks surveys at Cloudbridge be continued. As mentioned above, many studies of mixed species feeding flocks employ more intensive or sophisticated field and research methods, such as color-banding birds, continuous contact with particular mixed flocks over the course of each day, and experimental manipulation of the environment, etc. (Buskirk 1972; Sridhar et al. 2009). These methods may not be practicable at Cloudbridge. However, what Cloudbridge is well positioned to do is to support data collection on mixed species feeding flocks over the long term, ideally over multiple years, which few studies of mixed species feeding flocks can boast. Such long-term data collection has great potential to improve our knowledge of mixed species feeding flocks, especially in montane habitats and especially over different forest types with potentially significant conservation implications.

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Appendix A: 50m-interval Markers.

FIGURE A-1: MSF 1100m marker, Principal Trail, RIO Circuit.

FIGURE A-2: MSF 2350m marker, Rio Trail, RIO Circuit.

Appendix A: 50m-interval Markers.

FIGURE A-3: MSF 2850m marker, Heliconia Trail, RIO Circuit.

FIGURE A-4: MAM 1450 marker, Montaña Trail, MON Circuit.

Appendix B: Weather Classification Tables.

TABLE B-1. RAIN CLASS

Rain Class		Conditions
0	None	No rain.
1	Drizzle	Barely raining. Tiny raindrops, very sparse or erratic rainfall. Rain gear not necessary.
2	Light	Rain falling at a steady rate, but sparse. Would get soaked if out for an extended period without rain gear.
3	Moderate	Rain constant and dense. Would get soaked in minutes without rain gear.
4	Heavy	Raindrops large and falling with force. Streams forming on some trails. Would get soaked immediately without rain gear.
5	Severe	Storm conditions. Sheets of rain falling from the sky. Trails become creeks. Dangerous to be out at all.

TABLE B-2. WIND CLASS

Wind Class		Conditions
0	Calm	Calm. Smoke rises vertically.
1	Faint	Fog and smoke drift indicates wind direction. Leaves stationary.
2	Light	Wind felt on exposed skin. Leaves rustle.
3	Moderate	Leaves and small twigs constantly moving. Light flags extended.
		Dust and loose paper raised. Small branches begin to move.
4	Strong	Branches of a moderate size move. Small trees in leaf begin to sway.
		Large branches in motion. Umbrella use becomes difficult. Empty plastic bins tip over.
5	Severe	Whole trees in motion. Effort needed to walk against the wind.

TABLE B-3. CLOUD COVER CLASS

Cloud Class		Conditions
0	Clear	No clouds.
1	Mostly Clear	A few scattered clouds.
2	Partly Cloudy	An equal amount of clouds and clear sky.
3	Mostly Cloudy	More clouds than clear sky.
4	Overcast	Full cloud cover.
5	Misty	Low lying clouds (fog).

Appendix C: Two Largest/Most Diverse Mixed Flocks.

Table C-1. Largest Flock, 8:20am, 5 June 2019, RIO 1450m (Rio Trail).

Species.	Number.
Slate-throated Redstart	2
Red-headed Barbet	2
Hairy Woodpecker	1
Long-tailed Silky-Flycatcher	6
Spot-crowned Woodcreeper	2
Buff-throated Saltator	1
Barred Becard	1
Common Chlorospingus	4
Scarlet-thighed Dacnis	1
Red-faced Spinetail	1
Golden-bellied Flycatcher	1
Silver-throated Tanager	1

Table C-2. Second Largest Flock, 7:30am, 8 June 2019, RIO 1350m (Rio Trail).

Species.	Number.
Costa Rican Warbler	4
Barred Becard	1
Common Chlorospingus	1
Slate-throated Redstart	1
Red-headed Barbet	1
Tufted Flycatcher	1
Streak-breasted Treehunter	1
Red-faced Spinetail	1
Speckled Tanager	5
Spot-crowned Woodcreeper	1
Brown-capped Vireo	1