

BUGGIN' OUT: A STUDY OF ECTOPARASITE INTERACTIONS ON AVIAN HOSTS

ACROSS DEFORESTATION GRADIENTS

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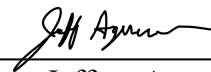
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Abstract

The functions and dynamics of ectoparasites within an ecosystem, as well as how they interact with and relate to their hosts, remain poorly understood. This study aims to further clarify our understanding of ectoparasite load in tropical birds, with a focus on Mesostigmatid mites and Ixodidae ticks at the FCAT Reserve in northwest Ecuador. Both mites and ticks are widespread ectoparasites that can be vectors for infectious disease and can also impact host productivity, however, mites are also considered commensalistic partners depending on the impact they have on their host. Previous anecdotal observations at FCAT have reported high tick and mite parasitism rates on birds captured in mist nets, but the environmental and ecological factors that shape these patterns are not well understood. This study characterizes mite and tick loads on birds captured in mist nets in relation to habitat types, year, and guild of the host bird species. The highest ectoparasite infestation rates were observed with mites in Pasture habitats (17.5%) and ticks in Old Growth (10.3%). Across years, we found a decline in both tick (11.0 per bird to 2.4 per bird) and mite load (24.66 per bird to 2.15 per bird) between the 2022 and 2023 seasons, which may be connected to the greater rainfall in the 2023 El Niño event. Comparisons of parasite load between foraging guilds show greatest rates of both tick (7.5%) and mite (15.0%) parasitism in Insectivores, which also experience the greatest

average tick load (9.2 per bird), while Frugivores encountered the greatest average mite load (26.5 per bird). The results of this study provide novel insights into host-parasite dynamics and their environmental drivers in a poorly studied, biodiversity hotspot.

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Introduction

Often unseen and frequently underestimated, parasites play a crucial role in the health and stability of ecosystems worldwide. While typically cast as villains due to their disease-spreading capabilities, parasites also offer valuable insights into ecosystem health and biodiversity. The literature contains a variety of hypotheses presenting potential interpretations of the host-parasite relationship, but Dobson et al. (2008) propose that a “healthy” ecosystem is one that is rich with parasitic species. The implication is that a healthy ecosystem will have an abundance of healthy hosts to parasitize, therefore the presence of parasites implies a healthy ecology (Juárez-Estrada et al., 2023, Marcogliese, 2005). A system with few parasites might indicate there are few or no viable hosts to parasitize, and conversely, a system with too many parasites implies that hosts are not healthy enough to avoid or resist parasites (Juárez-Estrada et al., 2023, Lymbery & Smit, 2023, Marcogliese, 2005, Selbach et al., 2022). Given the importance of preserving biodiversity and maintaining a functional food web, the relationship between parasites and their hosts presents an essential aspect of quantifying ecosystem health. By measuring anthropogenic pressures and understanding their impact on the delicate balance between parasites and hosts, we can gain crucial insights into the overall health of ecosystems (Marcogliese, 2005). This knowledge is pivotal for designing effective conservation strategies that not only safeguard biodiversity but also promote the resilience and stability of ecosystems in the face of human-driven changes.

Ticks are a highly influential organism in the ecosystems they inhabit. As hematophagous ectoparasites, ticks have the capacity to be vectors for infectious disease and introduce more human pathogens than all other arthropod groups. In addition to posing a risk for their host's

health, ticks can also have an impact on their host's productivity (Jongejan & Uilenberg, 2004, Møller, 1993). Aside from their direct impacts on their hosts, ticks can also serve as an indicator of their ecosystem's taxonomic composition, specifically their presence and density can be used to predict the presence and density of their hosts (De Mendonça et al., 2020, Oorebeek & Kleindorfer, 2008). Similarly, mites are also found on birds, though their relationship to their hosts is not as straightforward as the relationship between tick and host (Galván et al., 2012). While some studies determine that mites are commensalistic beneficiaries of their avian hosts' uropygial gland secretions, there appears to be a threshold of tolerance for feather mites (Galván et al., 2012, Proctor & Owens, 2000). An excessive load consuming too much feather-preserving coating can induce excessive preening and depluming, which could impact biological mechanisms, such as an individual's mate selection success, and even survival, through impeding their capacity for thermoregulation or flight (Proctor & Owens, 2000, Booth et al., 1993). Considering their wide-reaching influence on their hosts, it is important to further understand the factors that influence a bird's risk of parasitism and how that relationship changes with anthropogenic pressures. This study will investigate the relationship between parasite load and three factors: habitat, inter-annual variation, and host guild.

Parasite load has been documented to vary significantly across habitat type – specifically, across the old growth, deforestation, and subsequent regrowth gradient (S. Bugmyrin et al., 2010). Young forests are favorable for the development of hard ticks (Bugmyrin et al., 2013). Although previous hypotheses speculated that the population densities and distributions hard ticks would decrease and suffer following habitat loss and extreme fragmentation, studies found an initial decrease of tick population density immediately following Old Growth deforestation

(Bespyatova et al., 2006, Lutta and Shulman, 1954, S. Bugmyrin et al., 2010). Additional studies determined young, secondary forests fit the favorable biotope for the development of hard ticks (Lutta et al., 1959; Bobrovskikh, 1989, S. Bugmyrin et al., 2010). Following the initial decline, however, the population density reached seasonal maximum of young ticks as the successional forest regrew, which provides enough cover to support the more vulnerable preimaginal stages and sufficient height to snag passing hosts (S. Bugmyrin et al., 2010). When considering the association between mesostigmatid larval development and young forests, it stands to reason the parasites would thrive in the years following deforestation. To better understand these relationships, this study describes the variation in parasite load across common tropical habitat types: Pasture, Early Successional, Mid-Successional, and Old Growth. Given the demonstrated trends from previous work, we expected to observe similar associations between increased mesostigmatid parasite load on avian hosts associated with Pasture and Early Successional habitats.

Understanding temporal variation in ecological patterns is important because snapshot studies from a single time point can provide results that are misleading if interannual variation is high. For example, the larvae of the focal parasites of this study develop in deforested areas that might be highly sensitive to differences in temperature or precipitation. As such, one might expect that survival of larval and preimaginal mesostigmatid mites and ticks decrease in high rainfall years, for example if they are knocked off their habitual perching spots or flooded out of their habitats (Keesing et al., 2017). This study was conducted over three years, one of which (2023) was an El Niño year with elevated rainfall. We therefore predicted a decrease in the

presence of mesostigmatid parasites and rates of parasitism on their avian hosts during the 2023 season relative to other years.

In conjunction with climate and habitat, foraging behavior contributes to an individual's risk of parasitism (Dietsch, 2007). Mites are more prevalent on avian species that forage more frequently in lower vegetation strata, foraging at significantly lower heights compared to species with little to no parasites (Dietsch, 2007). Considering the unique niche partitioning of a tropical cloud forest, it stands to reason that birds of various foraging guilds will experience contrasting degrees of parasitism. In particular, we expected that guilds associated with foraging in the grass in pasture such as granivores and some insectivores, would have high rates of parasitism.

Materials and Methods

Collection Sites

The Andes, spanning 8,900 kilometers and peaking at 6,962 meters above sea level, are a biodiversity hotspot, characterized by a wide range of specialized habitats and microclimates. They support numerous endemic species uniquely adapted to these conditions (Särkinen et al., 2011; Myers et al., 2000). When habitats with niche specialization encounter drastic disruption, significant changes in a habitat's community and biodiversity are expected (Pendrill et al., 2022). Despite its importance for preserving biodiversity, the Andes have experienced a high degree of anthropogenic disturbance, resulting in the loss of nearly 75% of vital habitat to various purposes, such as agricultural-driven forest clearing or legal and illegal mining for precious metals and minerals (Hethcoat et al., 2019).

The Chocó biogeographic region, encompassing approximately 100,000 km² in the Esmeraldas province of Ecuador, ranges from 500-1,000m in elevation and is bordered by the

Pacific Ocean to the west. Characterized by its significant rainfall of 2-3.5m annually, peaking from January to May, and with a drier spell from October to December, the region's climate, alongside its geographic and oceanic conditions, influences distinct rainfall patterns across its latitudinal and altitudinal gradients. Within this system, cloud forests predominate, with a patchwork of pasture fragments that interrupt the continuity of mature old growth and secondary regrowth forests.

Agriculture, particularly for cacao, cattle, plantains, and African oil palms, has been a major driver of the region's forest fragmentation, accounting for approximately two-thirds of the land. Despite this, the diverse and complex ecosystem of the Chocó rainforest remains, supporting 360 recorded species, including 23-42 endemics, with 186 species documented in pioneer studies of species assemblages (Carrasco et al., 2013).

The Fundación para la Conservación de los Andes Tropicales (FCAT) is an Ecuadorian non-governmental organization (NGO) dedicated to protecting the land from further deforestation, restoring key species lost from anthropogenic disturbance, and furthering our understanding of such systems to better our conservation efforts. Within the 650-ha reserve owned and operated by FCAT, there is a vast array of flora and fauna that form a highly complex ecosystem. Prior to the purchase of FCAT's land, much of the property was used for agricultural activity, most commonly as a pasture for cattle grazing but also including cacao and coffee fields. This expansive deforestation of old growth forest has created a unique fragmentation pattern and vegetation regrowth gradient. The history of land use here, including its common use as cattle pasture, has led to unique ecological dynamics.

Fieldwork took place in summer months (May – August) of 2021, 2022 and 2023 at the FCAT Reserve. The FCAT Reserve contains a range of habitat types from recently abandoned pasture through successional forests to mature, intact forest. The FCAT Reserve has also hosted field courses and research projects that have captured birds in mist nets and assessed ectoparasite loads. The availability of these different habitat types and multi-year sampling efforts enabled me to investigate key questions related to habitat and inter-annual variation, as described below.

Sampling Methods

Avian hosts were captured across four habitat types, defined as Pasture, Early Successional, Mid Successional, and Old Growth (Table 1). Data collection in the 2021 season was conducted by Mary Elizabeth Barrow for six days of sampling, in the Pasture plots from July 28-30 and the Old Growth plots from August 3-5. Nicole Lussier and her 2022 team were responsible for that year's data collection, for 27 days from June 16–July 24. I joined Nicole and her team in the 2023 season, sampling for 35 days from June 21–August 3. Mist nets were set up in a rotating schedule through the four plot types, sampling in each plot type for two days at a time, four times. The nets were checked in twenty-minute intervals, and all birds captured were identified to species, weighed, and measured for standard morphological traits. I collected all ticks that were found on the birds and recorded them by individual hosts. Originally, I attempted to collect ticks in the environment by dragging a cloth through the tall grass. However, heavy rains during this period made sampling method unfeasible.

Table 1: *Descriptions of the four stages of the deforestation gradient at FCAT.*

<u>Habitat</u>	<u>Description</u>
Pasture	>5 years after clearing, dominated by tall grass and little canopy cover.
Early Successional	5-15 years post clearing, young trees, some shade/cover, minimal shrubbery/undergrowth.
Mid-Successional	15+ years post clearing, dominated by adult 20ft+ trees with majority shade cover and dense undergrowth.

Old Growth	Pristine forest with little to no previous anthropogenic influence.
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Climate Data

FCAT has a meteorological station on site with a Campbell Scientific CR300 datalogger, a Campbell Scientific HygroVUE10 probe for measuring temperature and relative humidity, a Met-One C034B windset anemometer for measuring wind speed/direction, an Apogee SP-110-SS pyranometer for measuring solar radiation, an Apogee SB-100 barometer for measuring atmospheric pressure, and a Texas Electronics TR-525M tipping bucket rain gauge for measuring rainfall amount. I used rainfall data from this station to determine rainfall levels in each of the three years of this study.

Classification of foraging guilds

I used published information in the Cornell Lab of Ornithology's All About Birds guide to classify the birds captured in mist nets into one of seven guilds: Frugivore, Insectivore, Nectarivore, Granivore, Generalist, Invertebrates, and Predatory (Table 2). To explore the contrast between birds with flexible foraging behaviors and those with stable routines, I classified each species according to their Primary and Secondary Foraging Guilds and identified their specific Niche Foraging Strata based on their most common and supplementary food sources and the habitats in which they occur (Cornell Lab of Ornithology, 2019). In addition to considering diet, we consider the preferred niche for engaging in foraging behaviors. In accordance with previous literature, we expect to observe higher prevalence of parasites on lower strata foragers, particularly Ground and Shrub (Dietsch, 2007).

Table 2: *Definitions of foraging guilds.*

<u>Foraging Guild</u>	<u>Primary food source</u>
Frugivore	fruits or other vegetation, i.e. Thraupidae (Tanagers, Euphonias, etc.)
Generalist	no strong preference for food source, i.e. Passerellidae (New World Sparrows)
Granivore	grasses, seeds, and grains, i.e. Fringillidae (True Finches)

Insectivore	insects and arthropods, i.e. Furnariidae (Ovenbirds), Tyrannidae (Flycatchers)
Invertebrates	small invertebrates such as crabs or snails, i.e. Cuculidae (Cuckoos)
Nectarivore	nectar from flowering plants, i.e. Trochilidae (Hummingbirds)
Carnivore	birds, small mammals, reptiles, etc., i.e. Strigidae (True Owls)

Collection and classification of parasites

Following removal from avian hosts, parasite specimens were stored in a 77% ethanol solution for preservation. After each day, the specimens were observed under a stereoscope to be identified by morphotype to separate into broad tick and mite categories.

Statistical Analyses

No statistical analyses were run, but descriptive data was compiled from datasets across three years. For each habitat, year, and foraging guild, we summarized the total birds captured, total individuals with ectoparasites, and the average parasite load. All results were analyzed, and all tables were generated using Microsoft Excel. Graphs were organized using Excel and Canva.

Results

Across three-years of data collection we captured a total of 1,120 birds, from which we recovered a total of 280 ticks and 2,505 mites. Of the 1,120 total birds sampled, 3.6% had at least one tick and 10.8% had at least one mite. Thus, overall rates of parasitism were relatively low.

I. Parasite Load by Habitat

Our first prediction was that we would observe variation in parasite load across habitats, with higher levels in pasture and early successional forest relative to late successional and mature forests. Table 4 provides detailed descriptive data on mite and tick occurrence in different habitat types. Pasture had the highest percentage of birds with at least one mite (17.5%) but the lowest number of mites per parasitized individual relative to forests. Conversely, ticks were most frequently present on Old Growth hosts (10.3% of birds had at least one tick), but a relatively

low number of ticks per parasitized individual; instead, pasture had the highest average number of ticks per parasitized individual. These results indicate that these two ectoparasites show contrasting and complex relationships with habitat type, and that there appears to be a trade-off between number of individuals infected vs. parasite load per infected individual for both mites and ticks.

Table 3: *Descriptive data of tick and mite load across habitat types at the FCAT Reserve in northwest Ecuador. Shown are the total number of birds captured by mist net in each habitat type, the total number (and %) of birds with at least one tick in each habitat, the total number (and %) of birds with at least one mite in each habitat, the total number of ticks detected among all birds, along with the average number of ticks per bird among those birds with at least one tick, and the total number of mites detected among all birds along with the average number of mites per bird among those birds with at least one tick.*

Habitat	Total birds captured	Total birds with ticks	Total birds with mites	Total ticks; (average/bird)	Total mites; (average/bird)
Pasture	513	22 (4.2%)	90 (17.5%)	187 (8.5)	1734 (9.5)
Early Successional	298	2 (.67%)	16 (5.4%)	5 (2.5)	381 (23.8)
Mid Successional	164	2 (1.2%)	5 (3.0%)	8 (4)	152 (30.4)
Old Growth	145	15 (10.3%)	10 (6.9%)	80 (5.3)	238 (23.8)
Total	1,120	41 (3.66%)	121 (10.8%)	280 (6.8)	2505 (20.7)

II. Parasite Load by Year/Climate

Our next hypothesis postulated that we would observe variation in parasitism dynamics across years, particularly during the increased rainfall during the 2023 El Niño year. Consistent with our predictions, we observed a sharp decrease in the average tick and mite load between 2022-23. Average tick load experienced a small decrease (11.0 vs 2.4), while mites underwent more substantial decline (24.66 vs 2.15). Though we captured more birds in 2023 than 2022 (713 vs. 357), the total birds with parasites decreased, a trend observed in both ticks (4.48% vs. 1.40%) and mites (27.73% vs. 2.81%).

Table 4: *Descriptive data of tick and mite load across years at FCAT. Shown are the total number of birds captured by mist net across three years, the total number (and %) of birds with at least one tick in each habitat, the total number (and %) of birds with at least one mite in each year, the total number of ticks detected among all birds, along with the average number of ticks per bird among those birds with at least one tick, and the total number of mites detected among all birds along with the average number of mites per bird among those birds with at least one tick.*

Year	Total birds captured	Total birds with ticks	Total birds with mites	Total ticks; (average/bird)	Total mites; (average/bird)
2021	50	15 (30.0%)	2 (4.0%)	80 (5.33)	21 (10.5)
2022	357	16 (4.48%)	99 (27.73%)	176 (11.0)	2441 (24.66)
2023	713	10 (1.40%)	20 (2.81%)	24 (2.4)	43 (2.15)
Total	1,120	41 (3.66%)	121 (10.8%)	280 (6.8)	2505 (20.7)

III. Parasite Load by Guild

Our final prediction was that parasite loads would vary between foraging guilds, above all that Granivores and Insectivores would experience greater rates of parasitism. Comparisons of parasite load between foraging guilds show greatest rates of both tick (7.5%) and mite (15.0%) parasitism in Insectivores, who also experience the greatest average tick load (9.2 per bird), while Frugivores encountered the greatest average mite load (26.5 per bird).

Table 5: *Descriptive data of variation in tick and mite load between Primary Foraging Guilds in birds captured at the FCAT Reserve. Shown are the total number of birds captured by mist net, organized by foraging guild, the total number (and %) of birds with at least one tick in each guild, the total number (and %) of birds with at least one mite in each guild, the total number of ticks detected among all birds, along with the average number of ticks per bird among those birds with at least one tick, and the total number of mites detected among all birds along with the average number of mites per bird among those birds with at least one tick Three guilds - Invertebrates (10 captures), Generalist (7 captures), and Carnivores (1 capture), had no parasites.*

Primary Guild	Total Cap	Total w/ ticks	Total w/ mites	Total ticks; (avg/indv)	Total mites; (avg/indv)
Insectivore	320	24 (7.5%)	48 (15.0%)	221 (9.2)	1132 (23.5)
Granivore	284	4 (1.4%)	21 (7.4%)	24 (6.0)	272 (12.9)
Frugivore	273	12 (4.4%)	38 (13.9%)	34 (2.83)	1007 (26.5)
Nectarivore	223	1 (0.44%)	14 (6.28%)	1 (1.0)	94 (6.71)

Discussion

The results of this study illustrate complex interactions between ectoparasites and avian hosts across a gradient of Neotropic rainforest deforestation, shedding light on the ecological dynamics influencing parasite loads in tropical birds. Overall, we detected fewer parasites on birds and fewer birds with parasites than expected. However, the majority of ectoparasite studies reviewed for this study had been conducted in temperate systems, so our understanding of how this differs from tropical systems is limited. Whether or not this indicates something about ecosystem health remains to be determined. We found some trends in parasite prevalence and intensity between habitat types, suggesting there may be some influence of habitat and environment on avian parasitic relationships. Though we expected to find the highest presence of ticks and mites in the Pasture overall, the association between parasite load and habitat was more nuanced. The Pasture, characterized by minimal canopy cover and increased grassland, produced high mite infestation but lower mite loads per affected individual. On the opposing end of the deforestation gradient, Old Growth, with denser undergrowth and sweeping canopy cover, had fewer individuals with ticks, but affected individuals still bore increased parasite loads. These complex patterns underscore the nature of these complex communities and the importance of habitat structure in mediating ecological interactions between hosts and their parasites. Our results suggest physical environment may significantly alter the risk of host species to parasitic infestations.

In the accumulation of three years of study, 1,120 birds were examined, revealing relatively low parasitism rates. Overall, only 3.6% of all birds captured had at least one tick, and only 10.8% had at least one mite. This demonstrates a very low level of ectoparasite presence;

thus, we can infer either the avian populations have evolved effective natural control mechanisms or environmental conditions do not favor high rates of parasite survival or reproduction.

Our results revealed variations in parasite loads across habitats, supporting initial predictions that habitat type influences ectoparasite prevalence and intensity. Pasture sites exhibited the highest percentage of birds with at least one mite (17.5%) but had the lowest average number of mites per infected bird, suggesting that while mite exposure is common in pastures, infestations remain controlled. In contrast, ticks had the highest prevalence in birds captured in Old Growth sites (10.3%), albeit still relatively low. This deviates from previous studies that had found the greatest density of ticks in deforested areas (S. Bugmyrin et al., 2010). Regardless, this trend demonstrates a habitat-specific influence on ectoparasite behavior and life cycles, where certain environments may facilitate higher exposure to parasites, but host density or behavior may limit the severity of infestations. Preening (and allopreening), sunning, and anting are all avian hygiene behaviors that help birds mitigate the intensity of their ectoparasite load (Proctor & Owens, 2000).

Temporal analysis revealed compelling variation in ectoparasite presence related to climatic variations, particularly during the increased rainfall associated with the El Niño event in 2023. Both tick and mite presence experienced a steep decline during this period, despite an increase in the number of birds captured. The average tick load decreased from 11.0 per bird in 2022 to 2.4 in 2023, and mite load dropped from 24.66 to 2.15, which suggests that increased rainfall affects ectoparasite populations. Our findings are substantiated by previous studies that have found parasites to be less abundant during periods of high rainfall (Keesing et al., 2017).

This is potentially explained by mechanisms such as increased humidity and rainfall impacting parasite survival or altering host-parasite interactions (Keesing et al., 2017). The decline could also be attributed to the removal of grazing cattle, an optimal host for a tick perched on a blade of grass, from the Pasture. Similar studies investigating the interactions between deer and tick prevalence found a decrease in ectoparasites in plots where their hosts, the deer, were removed or excluded (Gilbert et al., 2012, Stafford, 1993).

Analyzing variation in ectoparasite load between foraging guilds revealed that Insectivores and Frugivores experience the highest rates of parasites, with 7.5% and 15.0% of these guilds hosting ticks and mites, respectively. Previous studies have demonstrated similar trends, with individuals that foraging closer to the ground (in this case, primarily Insectivores) experience greater parasite prevalence (Dietsch, 2007). This suggests that the foraging behavior and habitat preference of these birds make them more susceptible to parasite infestations. Insectivores often forage in dense vegetation where ticks and mites may be more prevalent, and frugivores and could possibly exposed to higher parasite loads due to their movement patterns between different vegetation types. This highlights how ecological and behavioral factors influence parasitism rates, a relationship substantiated in previous studies (Dietsch, 2007).

While every effort was made to optimize the integrity of the results, it is important to consider some obstacles. The data for this project was collected over three years but was split with different overseers and collection duration, resulting in different sample sizes across the years. While every individual was thoroughly checked for ectoparasites, inspection was conducted by many individuals across multiple teams, so it is possible for there to have been discrepancies in ectoparasite detection. We had also intended on utilizing tick-dragging in 2023,

but consistent rain made it impossible to get an adequate sampling of the parasites. Additionally, this study would be strengthened by further examination of the comparisons between additional variables, such as degree of sociality or family. Understanding how different families or social structures (i.e. flock species, solitary, etc.) are related to ectoparasite infection would be useful, as many taxa of ectoparasites are host specific and social behaviors involving physical contact could control or magnify ectoparasite presence (Proctor & Owens, 2000).

The findings of our study suggest a relationship between ectoparasites and their avian hosts that merits further investigation. We observed nuanced patterns in parasite prevalence and intensity across different habitats, highlighting the influence of habitat structure on ecological interactions. Despite relatively low overall parasitism rates, our findings suggest that habitat type may shape the risk of host species to ectoparasitic infestations. Moreover, temporal and guild level analyses emphasize the dynamic nature of these interactions, with climatic variations and foraging guilds playing potentially important roles. While acknowledging limitations in data collection and the potential for further investigation into additional variables, this baseline study provides an important benchmark while contributing to a deeper understanding of the complex ecological dynamics governing avian-parasite relationships in tropical ecosystems.

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Appendix

Table S1: Descriptive data of primary and secondary foraging guilds. FR = frugivore, GR = granivore, GE = generalist, IN = insectivore, IV = invertebrates, NE = Nectarivore, CA = carnivore, NA= N/A.

Guild Pair	Total Cap	Total w/ ticks (avg/indv)	Total w/ mites (avg/indv)	Total ticks	Total mites
Frugivore- Insectivore	214	12 (2.83)	43 (23.19)	34	997
Insectivore- Frugivore	100	9 (5.11)	17 (24.47)	46	416
Insectivore- Invertebrates	10	5 (12.6)	0 (0)	63	0
Nectarivore- Insectivore	216	1 (1.0)	14 (6.71)	1	94
Granivore- Generalist	60	1 (10.0)	2 (13.0)	10	26
Granivore- Insectivore	10	1 (10.0)	1 (18.0)	10	18
Insectivore- Carnivore	10	1 (1.0)	0 (0)	1	0
Insectivore- Granivore	7	0 (0)	1 (100.0)	0	100
Invertebrates- Frugivore or Granivore	6	0 (0)	0 (0)	0	0
Frugivore- Nectarivore	7	0 (0)	0 (0)	0	0
Frugivore- Generalist or Granivore	12	0 (0)	0 (0)	0	0

Figure S1: Descriptive pie chart demonstrating the composition of captures in Pasture based on foraging guild. Total captured in Pasture = 513. Total captured overall = 1,120.

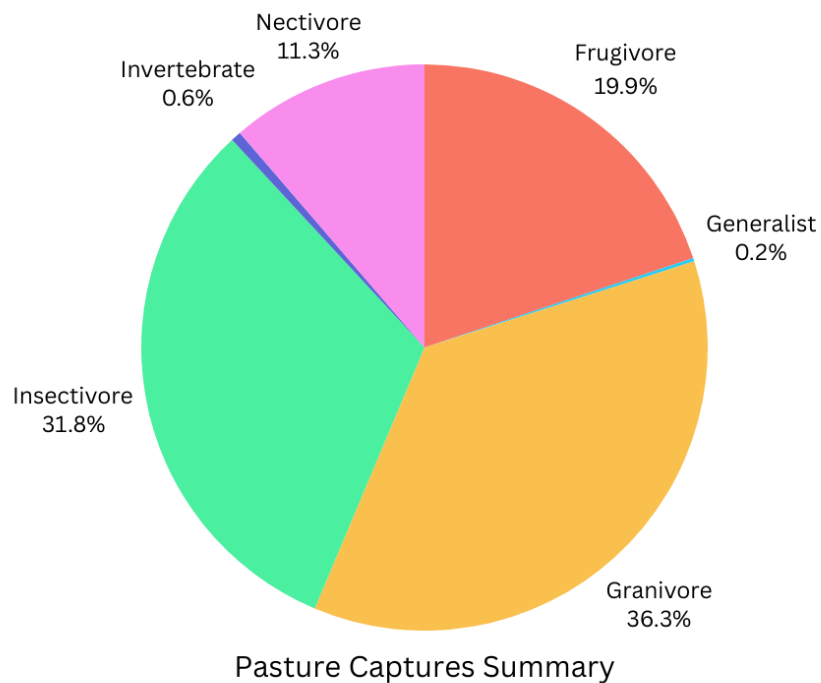


Figure S2: Descriptive pie chart demonstrating the composition of captures in Early Successional based on foraging guild. Total captured in Early Successional = 298. Total captured overall = 1,120.

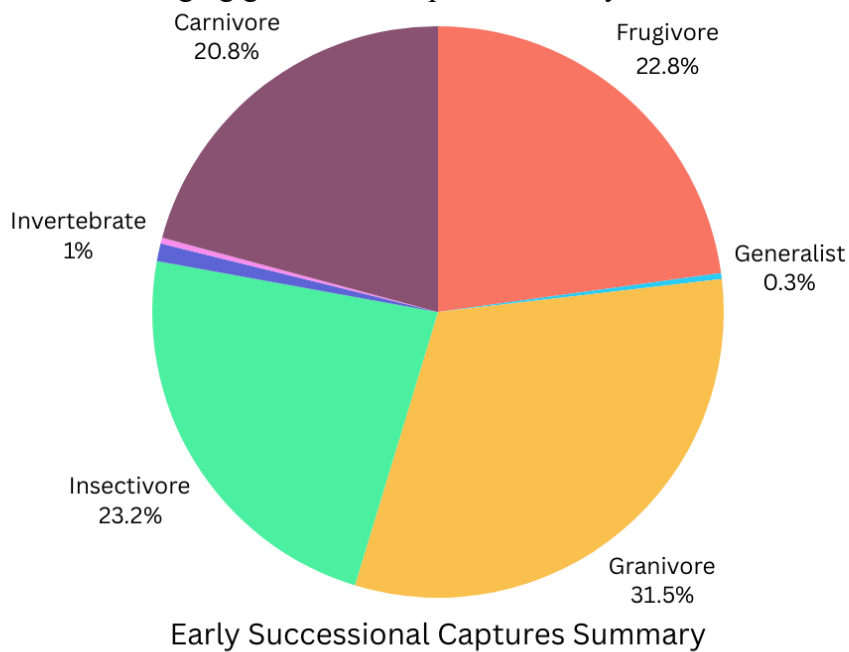


Figure S3: Descriptive pie chart demonstrating the composition of captures in Mid Successional based on foraging guild. Total captured in Mid Successional = 164. Total captured overall = 1,120.

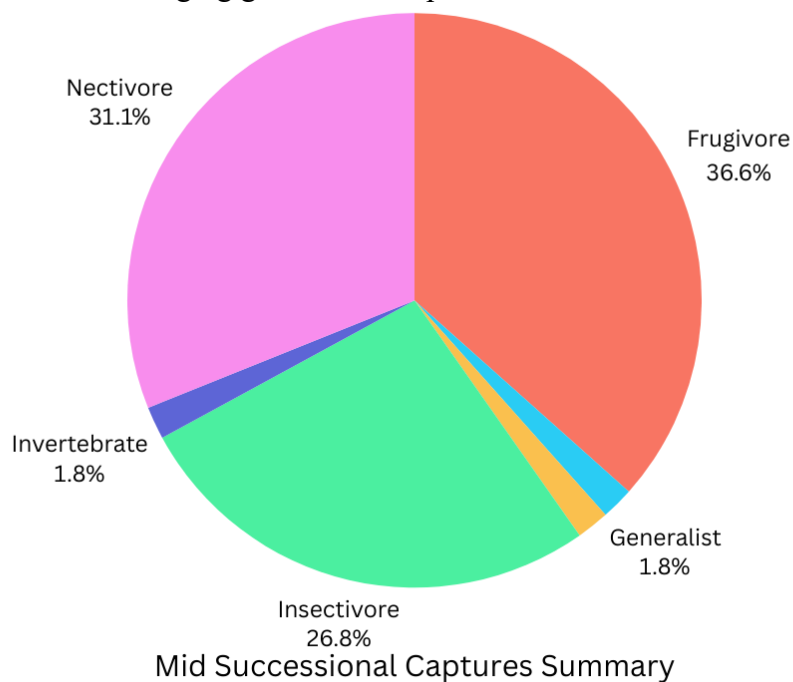


Figure S4: Descriptive pie chart demonstrating the composition of captures in Mid Successional based on foraging guild. Total captured in Mid Successional = 164. Total captured overall = 1,120.

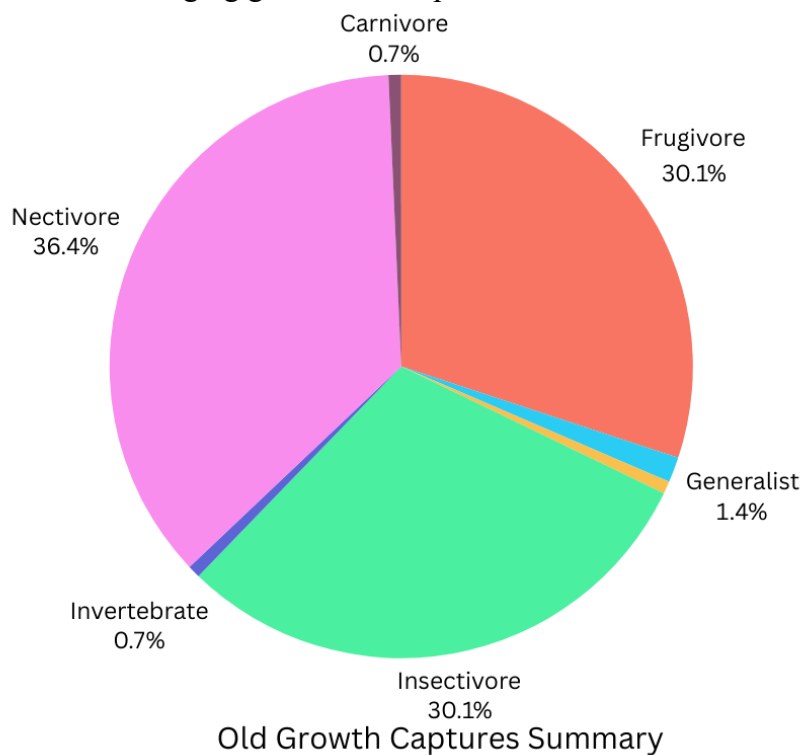


Table S2: Descriptive table of all species captured and their Primary Guild (PGuild), Secondary Guild (SGuild), Foraging Niche, Total Captured, and Total Parasitized.

Species	PGuild	SGuild	Niche	Total Captured	Total Parasitized
Bananaquit	Nectivore	Insectivore	Shrub	33	7
Band-Backed Wren	Insectivore	N/A	Generalist	1	0
Band-Tailed Barbthroat	Nectivore	Insectivore	Understory	26	0
Bay Wren	Insectivore	N/A	Understory	4	1
Bay-Headed Tanager	Frugivore	Insectivore	Understory	3	2
Bicolored Antbird	Insectivore	N/A	Ground	7	1
Black-Crowned Antshrike	Insectivore	N/A	Understory	3	0
Black-Faced Dacnis	Frugivore	Insectivore	Canopy	2	1
Black-Tailed Flycatcher	Insectivore	N/A	Shrub	1	0
Blue Ground Dove	Granivore	Insectivore	Ground	2	0
Blue-And-White Swallow	Insectivore	N/A	Open	3	2
Blue-Black Grassquit	Granivore	Insectivore	Ground	7	0
Blue-Black Grosbeak	Frugivore	Insectivore	Understory	3	1
Blue-Capped Manakin	Frugivore	Insectivore	Understory	16	1
Blue-Chested Hummingbird	Nectivore	Insectivore	Shrub	18	0
Blue-Fronted Parrotlet	Frugivore	N/A	Upper Canopy	1	2
Blue-Gray Tanager	Frugivore	Insectivore	Generalist	9	0
Blue-Necked Tanager	Frugivore	Insectivore	Canopy	8	0
Bran-Colored Flycatcher	Insectivore	Frugivore	Ground	12	0
Bright-Rumped Attila	Invertebrates	Frugivore	Lower Canopy	2	2
Brown-Billed Scythebill	Insectivore	N/A	Understory	1	0
Buff-Rumped Warbler	Insectivore	N/A	Understory	6	2
Buff-Throated Saltator	Frugivore	Generalist	Understory	8	0
Checker-Throated Stipplethroat	Insectivore	N/A	Generalist	4	0
Chestnut-Backed Antbird	Invertebrates	N/A	Shrub	4	0
Chestnut-Throated Seedeater	Granivore	N/A	Ground	1	2
Chivi Vireo	Insectivore	Frugivore	Lower Canopy	19	0
Choco Manakin	Frugivore	Insectivore	Lower Canopy	6	0
Choco Tyrannulet	Frugivore	Insectivore	Lower Canopy	15	0
Choco Warbler	Insectivore	N/A	Understory	3	0
Cinnamon Becard	Insectivore	Frugivore	Understory	3	4
Collared Aracari	Frugivore	Insectivore	Upper Canopy	2	1

Common Tody Flycatcher	Insectivore	N/A	Generalist	15	2
Crowned Woodnymph	Nectivore	Insectivore	Lower Canopy	13	0
Dot-Winged Antwren	Insectivore	N/A	Ground	2	1
Dull-Colored Grassquit	Granivore	N/A	Understory	75	0
Dusky Antbird	Insectivore	N/A	Ground	1	5
Dusky Pigeon	N/A	N/A	Upper Canopy	1	1
Dusky-Capped Flycatcher	Insectivore	Granivore	Generalist	1	1
Ecuadorian Thrush	Frugivore	Insectivore	Understory	5	8
Flame-Rumped Tanager	Frugivore	Insectivore	Shrub	21	0
Flycatcher Sp.	Insectivore	N/A	Generalist	1	0
Golden-Olive Woodpecker	Insectivore	Frugivore	Lower Canopy	2	0
Gray-And-Gold Warbler	Insectivore	N/A	Understory	1	1
Gray-Breasted Martin	Insectivore	N/A	Open	1	4
Great Antshrike	Invertebrates	Granivore	Ground	1	1
Green Honeycreeper	Frugivore	Nectivore	Lower Canopy	7	1
Green Manakin	Frugivore	Insectivore	Lower Canopy	3	0
Green Thorntail	Nectivore	Insectivore	Lower Canopy	2	0
Green-Crowned Brilliant	Nectivore	Insectivore	Lower Canopy	4	0
Groove-Billed Ani	Insectivore	N/A	Ground	1	0
House Wren	Insectivore	N/A	Generalist	35	0
Large-Billed Seed-Finch	Granivore	Insectivore	Shrub	1	1
Long-Billed Starthroat	Nectivore	Insectivore	Lower Canopy	1	0
Mottled Owl	Carnivore	N/A	Generalist	1	0
Northern Schiffornis	Frugivore	Insectivore	Ground	7	12
Ocellated Antbird	Insectivore	N/A	Ground	1	0
Ochre-Bellied Flycatcher	Insectivore	Frugivore	Generalist	27	1
Ochre-Throated Foliage Gleaner	Insectivore	N/A	Ground	2	0
Olivaceous Piculet	Insectivore	N/A	Understory	5	1
Olivaceous Woodcreeper	Insectivore	N/A	Lower Canopy	4	1
Olive-Crowned Yellowthroat	Insectivore	N/A	Open	7	7
Olive-Sided Flycatcher	Insectivore	N/A	Open	1	0
Olive-Striped Flycatcher	Frugivore	Insectivore	Understory	30	0
Orange-Bellied Euphonia	Frugivore	Insectivore	Lower Canopy	27	0
Orange-Billed Sparrow	Generalist	N/A	Understory	7	1

Orange-Crowned Euphonia	Frugivore	Insectivore	Lower Canopy	4	0
Orange-Fronted Barbet	Frugivore	Insectivore	Generalist	1	5
Ornate Flycatcher	Insectivore	Granivore	Open	5	0
Pacific Antwren	Insectivore	N/A	Shrub	9	9
Pacific Parrotlet	Frugivore	Granivore	Shrub	1	0
Pale-Vented Thrush	Frugivore	Granivore	Understory	2	3
Palm Tanager	Frugivore	Insectivore	Understory	4	1
Plain Xenops	Insectivore	N/A	Understory	2	1
Plain-Brown Woodcreeper	Insectivore	Invertebrates	Understory	10	1
Purple-Chested Hummingbird	Nectivore	N/A	Shrub	1	0
Purple-Crowned Fairy	Nectivore	Insectivore	Lower Canopy	1	0
Red-Capped Manakin	Frugivore	Insectivore	Understory	15	3
Red-Faced Spinetail	Insectivore	N/A	Understory	1	0
Ruddy Pigeon	Frugivore	N/A	Upper Canopy	2	5
Rufous Piha	Insectivore	Frugivore	Lower Canopy	1	0
Rufous-Tailed Hummingbird	Nectivore	Insectivore	Generalist	20	0
Rusty-Margined Flycatcher	Insectivore	Granivore	Generalist	1	3
Sapayoa	Insectivore	Frugivore	Understory	1	0
Scale-Crested Pygmy Tyrant	Insectivore	N/A	Understory	3	0
Scaly-Breasted Wren	Insectivore	N/A	Ground	3	0
Silver-Throated Tanager	Frugivore	Insectivore	Shrub	4	0
Slaty Antwren	Insectivore	N/A	Shrub	3	0
Slaty Spinetail	Insectivore	N/A	Shrub	29	0
Smooth-Billed Ani	Invertebrates	Frugivore	Open	3	0
Sooty-Crowned Flycatcher	Insectivore	N/A	Generalist	1	0
Sooty-Headed Tyrannulet	Insectivore	Frugivore	Upper Canopy	4	1
Southern Beardless Tyrannulet	Insectivore	Frugivore	Shrub	12	0
Southern Mouse-Colored Tyrannulet	Insectivore	Frugivore	Shrub	1	3
Southern Rough-Winged Swallow	Insectivore	N/A	Open	9	0
Spotted Woodcreeper	Insectivore	Carnivore	Generalist	4	0
Streak-Headed Woodcreeper	Insectivore	Frugivore	Ground	5	3
Streaked Xenops	Insectivore	N/A	Understory	1	4
Stripe-Throated Hermit	Nectivore	N/A	Shrub	6	1

Sulphur-Rumped Flycatcher	Insectivore	N/A	Understory	5	3
Tawny-Crested Tanager	Insectivore	N/A	Generalist	1	1
Thick-Billed Euphonia	Frugivore	N/A	Lower Canopy	38	0
Thick-Billed Seed-Finch	Granivore	N/A	Shrub	63	0
Thick-Billed Seedeater	Granivore	Frugivore	Understory	1	0
Tropical Kingbird	Insectivore	Frugivore	Open	2	0
Variable Seedeater	Granivore	Generalist	Ground	60	0
Violet-Bellied Hummingbird	Nectivore	Insectivore	Understory	12	0
Warbler Sp.	N/A	N/A	N/A	1	3
Wedge-Billed Woodcreeper	Insectivore	Frugivore	Understory	5	3
White-Bearded Manakin	Frugivore	Insectivore	Understory	29	0
White-Flanked Antwren	Insectivore	N/A	Shrub	3	1
White-Shouldered Tanager	Insectivore	Frugivore	Understory	1	3
White-Thighed Swallow	Insectivore	N/A	Open	2	0
White-Throated Spadebill	Insectivore	N/A	Ground	4	0
White-Tipped Sicklebill	Nectivore	Insectivore	Understory	12	0
White-Whiskered Hermit	Nectivore	Insectivore	Understory	74	1
White-Whiskered Puffbird	Insectivore	Carnivore	Ground	6	2
Yellow-Bellied Elaenia	Insectivore	Frugivore	Generalist	4	0
Yellow-Bellied Seedeater	Granivore	N/A	Open	70	1
Yellow-Bellied Siskin	Granivore	N/A	Lower Canopy	4	0
Yellow-Crowned Tyrannulet	Insectivore	N/A	Generalist	7	0
Yellow-Olive Flatbill	Insectivore	Frugivore	Understory	1	0