UNIVERSIDAD SAN FRANCISCO DE QUITO USFQ

Colegio de Ciencias Biológicas y Ambientales

Diet Composition of the Galápagos Lava Lizards: (Iguania: Tropiduridae: *Microlophus*)

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RESUMEN

Este estudio buscó describir las dietas de seis lagartijas de lava *Microlophus* diferentes de las islas Galápagos e identificar las especies de hormigas presentes en las dietas de las lagartijas de lava para determinar la influencia antropogénica en las dietas de estos reptiles. Dada la historia evolutiva alopátrica de las lagartijas de lava de Galápagos, la recolección de muestras fecales de lagartijas de lava ocurrió en seis islas diferentes del archipiélago (una especie de *Microlophus* por isla). Los resultados muestran que entre 85 y 95 % de las presas consumidas por las lagartijas de lava de Galápagos son himenópteros, mientras que otras presas fueron raras y escasas. De todos los himenópteros consumidos, entre 92 y 99 % fueron hormigas, lo que sugiere que las lagartijas *Microlophus* de Galápagos son principalmente mirmecófagas, pero de manera oportunista consumen otros tipos de presas. El 99,4 % de todas las hormigas consumidas por las lagartijas fueron especies de hormigas introducidas, lo que sugiere que las especies de hormigas introducidas en el Archipiélago son un componente clave en la dieta de las lagartijas de lava de Galápagos.

Palabras clave: Galápagos, lagartijas de lava, *Microlophus*, hormigas introducidas, dietas, contenidos fecales.

ABSTRACT

This study sought to describe the diets of six different *Microlophus* lava lizards of the Galápagos islands and identify ant species present in lava lizard diets to determine anthropogenic influence on *Microlophus* lizards' diets. Given the allopatric evolutionary history of Galápagos lava lizards, the collection of fecal samples from lava lizards occurred on six different islands of the Archipelago (one *Microlophus* species per island). The results show that between 85 and 95 % of consumed prey by Galápagos lava lizards are hymenopterans, while other prey items were rare and scarce. Of all hymenopterans consumed, between 92 and 99% were ants, suggesting that *Microlophus* lizards of the Galápagos are mainly myrmecophagous, but will opportunistically consume other types of prey. The 99,4 % of all ants consumed by the lizards were introduced ant species, suggesting that introduced ant species in the Archipelago are a key component in the diet of Galápagos lava lizards.

Key words: Galápagos, lava lizards, *Microlophus*, introduced ants, diets, fecal contents.

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INTRODUCTION

Lava lizards (*Microlophus*) are coastal species that inhabit rocky shores, sand dunes, and adjacent uplands (Rowe et al., 2021). The genus contains 23 species that inhabit South America, 10 of which are endemic to the Galápagos Islands (Benavides et al., 2009). Lava lizards of the Galápagos are considered to have an asymmetrical radiation which produced an allopatric speciation of *Microlophus* lizards (Kizirian et al., 2004). This study focused on the diet of six species of Galápagos lava lizards which include *M. albemarlensis*, *M. bivittatus*, *M. duncanensis*, *M. grayii*, *M. indefatigabilis,* and *M. jacobi*.

Prior studies have been conducted to characterize the diet of lava lizards that inhabit continental South America. A study on *M. occipitalis*, a species that inhabits the coast of Ecuador and Peru, found that the most abundant prey items were Hymenoptera (58,9 %), Coleoptera (15,2 %), and Homoptera (4,3%) (Chávez-Villavicencio et al., 2018). Remarkably, all Hymenoptera consumed by *M. occipitalis* were ants.

A study on *M. stolzmanni* (endemic lava lizard of the dry forest of northern Peru) found that this lizard is a generalist semi-herbivorous reptile that feeds mainly on colony building insects (e.g., ants and termites) and sedentary prey (e.g., larvae from lepidopterans), but rarely feeds on mobile prey (Beuttner & Koch, 2019). Also, plant material becomes a more important food resource for this lizard as individuals mature (Beuttner & Koch, 2019).

The diets of the Galápagos *Microlophus* lizards have not been thoroughly studied to date. Lewbart et al. (2017) reported that lava lizards from the Galápagos are mainly insectivores, but will opportunistically consume centipedes, spiders, and even other small vertebrates (such as geckos, tails of conspecifics, and smaller conspecifics; see also Stebbins et al., 1967). Additionally, Van Denburgh & Slevin (1913) noted that several *Microlophus* individuals also consume plant structures such as seeds, leaves, flowers, and fruits. understood. Studies on San

Cristóbal lava lizard (M. bivittatus) report that the species feeds on small insects such as ants, and occasionally on moths, spiders, crickets, and dragonflies (Moore et al., 2017). Additionally, M. bivittatus has also been observed foraging on plant material such as leaflets of the Jerusalem thorn (Parkinsonia aculeata) and fruits of the Palo Santo (Bursera graveolens) (Moore et al., 2017).

Another study involving Galápagos lava lizards found that 8,4 % of sampled individuals (corresponding to 7 out of 9 species of *Microlophus* lizards studied) carried pollen from 10 different plant species, of which 8 were native plant species of the Galápagos (Hervías-Parejo et al., 2020).

However, the proportions of food items ingested by Galápagos lava lizards (including both from plant and animal origin) are poorly understood. Given that most studies report ants as a common prey item for *Microlophus* lizards (Chávez-Villavicencio et al., 2018; Beuttner & Koch, 2019; Lewbart et al. 2017; Moore et al., 2017), and taking in consideration that ants are ecological diverse (Tiede et al., 2017), this study will make emphasis characterizing ant species (Hymenoptera: Formicidae) found on fecal samples of lava lizards (Lach et al., 2010). Ants are of particular interest because they may increase or decrease in abundance in relation to a disturbance in their ecosystem (Andersen & Majer, 2004). In fact, ants can be used as an indicator of anthropogenic disturbance of the Galápagos islands since invasive ant species have shown to have considerable effects on native biodiversity (Ujiyama & Tsuji, 2018).

With the ongoing increase in human population and tourist activities in the Galápagos Islands, the chances of accidental introductions of exotic species increase (Watson et al., 2010). As a consequence, not only do the natural ecosystems degrade, but the increase of human activities is expected to become a continuous vector of introduced species, specially of small invertebrates (Toral-Granda et al., 2017). In fact, it has been reported that the introduction of new species is the main threat for terrestrial native taxa of the Galápagos (Snell et al., 2002).

For example, only in Floreana Island alone, there are at least 14 introduced ant species that belong to the following genera: *Strumigenys*, *Tapinoma*, *Solenopsis*, *Paratrechina*, *Monomorium*, *Tetramorium*, *Wasmannia*, and *Cardiocondyla* (Aesch & Cherix, 2005). More than 30 introduced species have been reported in the Archipelago (see Appendix I.)

It has also been documented that at least two ants introduced to the Galápagos (*Wasmannia auropunctata* and *Solenopsis geminata*) are directly affecting native biota (Causton et al., 2006). *W. auropunctata* has been classified as one of the worst 100 invaders in the world by the Species Specialist Group of International Union for Conservation of Nature (IUCN) (Lowe et al., 2002). Some characteristics that make *W. auropunctata* a successful invasive species is its polyphagous feeding habits, lack of intraspecific aggression, high interspecific aggression, and its capability of adaptation to a broad type of habitats and environments (Ulloa-Chacón & Cherix 1990). In the Galápagos Islands, *W. auropunctata* has colonized Isabela, Floreana, Santa Cruz, San Cristobal, Pinzón, Santiago, Santa Fe, and Marchena Islands (Silberglied, 1972). In general terms, *W. auropunctata* has negative impacts on nesting activities of tortoises (Lubin, 1985), and it also negatively affects the biodiversity of native invertebrates (Clark et al., 1982).

On the other hand, *Solenopsis geminata* was first registered in the Galápagos Islands in 1891 in San Cristóbal (Brandão & Paiva, 1994). Nowadays, *S. geminata* can be found on 7 islands and 11 islets of the Archipelago (Wauters et al., 2014). *S. geminata* is a predatory ant, and it has been reported to prey on native Lepidoptera and Hemiptera of the Galápagos (Wauters et al., 2018). Also, *S. geminata* can obliterate and displace ants from places they were previously abundant (von Aesch & Cherix, 2005).

Hypothesis

Urbanization and high human populated areas tend to increase the availability of food in both terrestrial and aquatic systems (El-Sabaawi, 2018). Consequently, it has been suggested that some invasive species can take advantage of the increase of food availability and displace native species in urbanized areas (Santana et al., 2020). For example, invasive ant species displace native species by making better use of resources and being more territorial than native species (Lach et al., 2010). For this reason, it is hypothesized that fecal contents of lava lizards (*M. duncanensis* and *M. jacobi*) that inhabit unpopulated (by humans) islands (Pinzon Island and Santiago respectively) with low levels of human disturbance will have an overall low abundance of invasive ant species in their diets. In comparison, it is expected to see high levels of abundance of invasive ants from lizards that inhabit highly urbanized and touristic islands (Isabela, Santa Cruz, Floreana, San Cristobal).

Within this described state of the art, this study has the following aims: 1) to describe, characterize and compare the diets of six lava lizards endemic to the Galápagos; 2) to identify ant species present in lava lizard diets. Ants can be used to determine anthropogenic influence on *Microlophus* lizards' diets, we also tested the hypothesis that fecal contents of lava lizards (M. duncanensis and M. jacobi) that inhabit unpopulated (by humans) islands (Pinzon Island and Santiago respectively) with low levels of human disturbance will have an overall low abundance of invasive ant species in their diets. In comparison, it is expected to see high levels of abundance of invasive ants from lizards that inhabit highly urbanized and touristic islands (Isabela, Santa Cruz, Floreana, San Cristobal).

MATERIALS & METHODS

Sampling

Field work took place on six islands (nine localities) of the Galápagos Archipelago (Fig. 1). Feces from lava lizards were sampled from December 2018 to January 2019 and from December 2019 to January 2020. Fecal material was collected from leaves, soil, branches, trunks, and leaf litter along linear transects. At each locality, sampling consisted of three non-overlapping linear transects of 4 m x 120 m. Sampling and feces collection occurred between 8 am and 6 pm. Every fecal sample was collected and stored in 96 % ethanol for its subsequent analysis in the laboratory.

Isabela Island

Sampling at Isabela Island occurred at two different localities which are Centro de Crianza de Tortugas Gigantes (Centro de Crianza), located at South Isabela, and Muro de Lágrimas, which is also located on the Southern coast of Isabela and its further east than Centro de Crianza.

Santa Cruz Island

For Santa Cruz, fecal samples were collected on 4 different sites. The first site of collection was Los Alemanes, which is a beach located on the south coast of Santa Cruz. The second sampled locality was Galápagos National Park (GNP), located in the center and inner part of Santa Cruz. The third location sampled was Tortuga Bay, which is another beach located on the South of Santa Cruz and further east than Los Alemanes locality. Finally, El Garrapatero, the fourth sampled location in Santa Cruz is located on a beach on the southwest section of the island.

Other Islands

There was only one sampled location for Floreana, Pinzon, San Cristobal, and Santiago Islands. In Floreana, sampling occurred in La Loberia beach, while in Pinzon island, sampling occurred in Playa Escondida beach. For San Cristobal and Santiago islands, sampling occurred in "Centro de Interpretación Ambiental Gianni Arismendy" and in Playa Espumilla respectively. The following map shows all sampling locations that were made for this study.

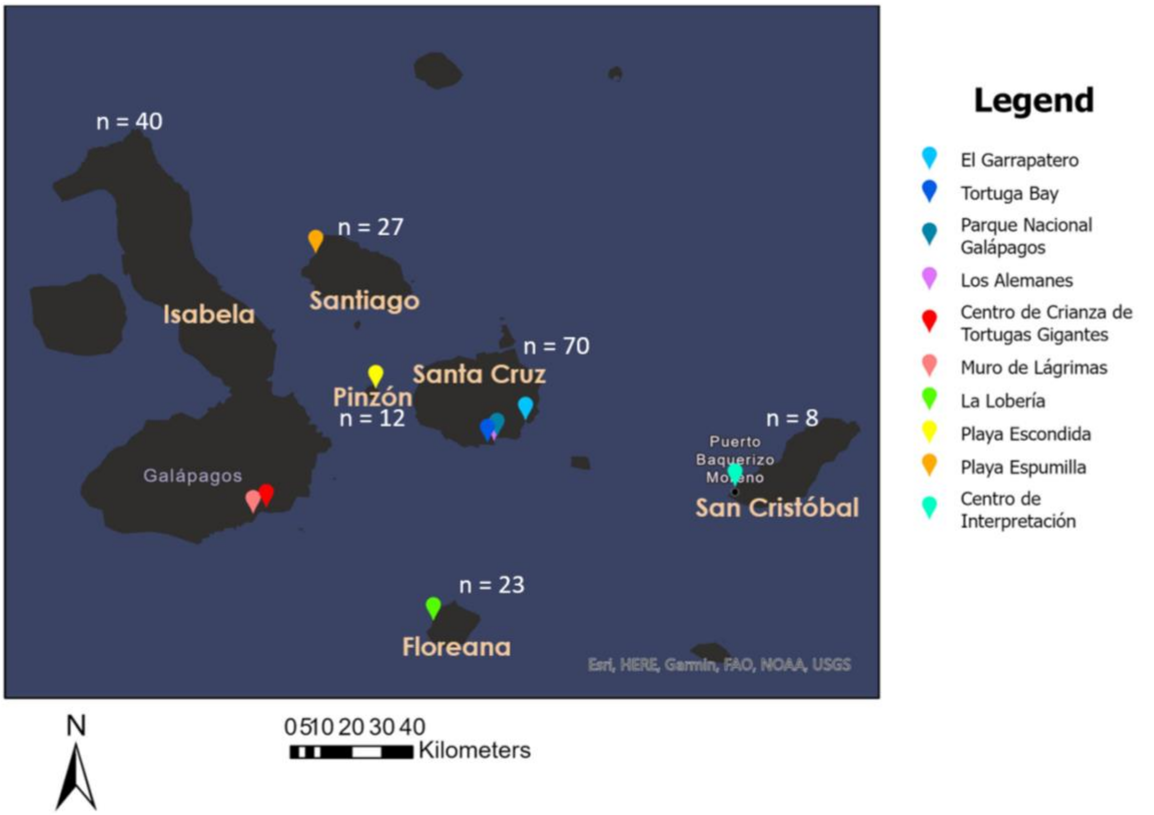

Fig 1. *Sampling localities in the Galápagos Islands and the corresponding species of lava lizard*

Dietary Analysis

A total of 180 fecal samples were collected for this study. From these 180 fecal samples collected, 70 were collected in Santa Cruz, 40 in Isabela, 27 in Santiago, 23 in Floreana, 12 in Pinzón, and 8 in San Cristóbal. The content of every fecal sample collected was analyzed under a stereomicroscope and invertebrates were separated from the rest of organic matter (such as plant material or skin molt from invertebrates). Invertebrates were quantified and identified up to order level. However, ants (Formicidae) were sorted into morphospecies and identified to the lowest possible taxonomic level. Given that most specimens had been partially digested after passing through the lizards' gut, to avoid confusion, only heads were used as a reliable indicator of the occurrence of an ant on a sample. We used Fernández (2003) to identify ants to genus and keys available at AntWeb (2022) and AntWiki to species level.

Data Analysis

Overall diversity of the diets of every *Microlophus* was estimated using the Simpson-Index (B); we also calculated an Inverse Simpson-Index (B') to compare our results with data from continental *Microlophus* species. Values for B vary between 0 and 1, where values closer to 0 mean that overall diversity is high (representing a generalist diet), and values closer to 1 represent low diversity (which implies that there is an exclusive use of one or few prey items) (Somerfield et al., 2008). Values of B' can range from 1 to *n*, where the higher the value, the higher the diversity (meaning that there is considerable variation in prey preferences, generalist). Both B and B' indexes take into consideration relative species richness and evenness for estimating overall diversity.

The distances of sampled sites to the closest urban area were estimated using Google Earth Pro. Linear plots were built using RStudio for comparing overall ant diversity and distances to sampled sites for determining if ant diversity found on fecal samples had a correlation with nearby urban areas. The locality 'Los Alemanes' was excluded from this analysis because there was only one fecal sample obtained from this location.

For determining the level of similarity between the diets of each Galápagos lizard species studied, a dendrogram was built using the UPGMA approach. The UPGMA approach assumes a constant substitution rate over time (also known as molecular clock hypothesis) (Weiß & Göker, 2011). Therefore, the Jaccard index was used as a parameter for building the dendrogram between ant communities consumed by each lava lizard studied (Moreno, 2001).

The Jaccard index is a statistical coefficient that determines the similarity between *n* number of sites based on the number of species that are found at each site Values for Jaccard index vary between 0 and 1, where values closer to 0 represent that species composition between the studied sites is very different, whereas values closer to 1 mean that the analyzed sites have similar species composition (Moreno, 2001).

RESULTS

A total of 15 different prey items (orders) were found to be consumed by Galápagos lava lizards. Note that Hymenoptera is, by much, the most frequent order consumed (Fig. 2). The most consumed prey items by *Microlophus* lava lizards of the Galápagos are: hymenopterans (85-95 %), followed by coleopterans (4-10 %), and plant structures (0-6 %) (Fig. 2). Other consumed prey items were rare and scarce. The vast majority of prey items identified were insects (11 out of 15 prey items), and 2 out of 15 prey items found were arachnids, suggesting that the main components of the diets of *Microlophus* lava lizards of the Galápagos are arthropods.

Among hymenopterans, ants (Formicidae) were the most common prey (92–99%). Other hymenopterans, such as bees and wasps, represented between 1–8 % of prey (Fig. 3).

Overall, 18 different ant species were identified on fecal samples. Ant species consumption varied depending on the *Microlophus* species and location (see Fig. 4). The most common prey were *Tapinoma melanocephalum* (44 %), *Tetramorium* spp. (16 %), and *Paratrechina longicornis* (15%). This relative abundance was estimated adding up the total amount of all ants consumed by all studied lava lizards. Although, it appears that *T. melanocephalum* is the most abundant ant species found in fecal samples, we note that this results is heavily influenced by the 2536 individuals of this ant species consumed by *M. indefatigabilis* (Santa Cruz lava lizard); *T. melanocephalum* was not a very abundant prey in other lava lizards diets. Other abundant ant species consumed by Galápagos lava lizards include *Camponotus zonatus* and *Monomorium floricola*, both with a relative abundance of 6 %.

Specifically, it was found that for *M. grayii*, the most consumed ant species include *Tetramorium* spp. (46 %), *Paratrechina longicornis* (21 %) and *Tapinoma melanocephalum* (9 %). For *M. albemarlensis*, most consumed ant species were *Paratrechina longicornis* (47

%), *Tapinoma melanocephalum* (15 %) and *Tetramorium* spp. (10 %). For *M. duncanensis*, the most consumed ant species were *Tetramorium* spp. (79 %), *Camponotus zonatus* (10 %), and *Nylanderia steinheili* (5 %). For *M. bivittatus*, the most consumed ant species include "Myr 21" (34 %), *Solenopsis* spp. (30 %) and *Paratrechina longicornis* (10 %). For *M. indefatigabilis*, the most consumed ant species were *T. melanocephalum* (59 %), *Paratrechina longicornis* (14 %), and *Monomorium floricola* (8 %). Finally, for *M. jacobi*, the most consumed ant species were *Tetramorium* spp. (66 %), *Solenopsis* spp. (19 %), and *T. melanocephalum* (4 %).

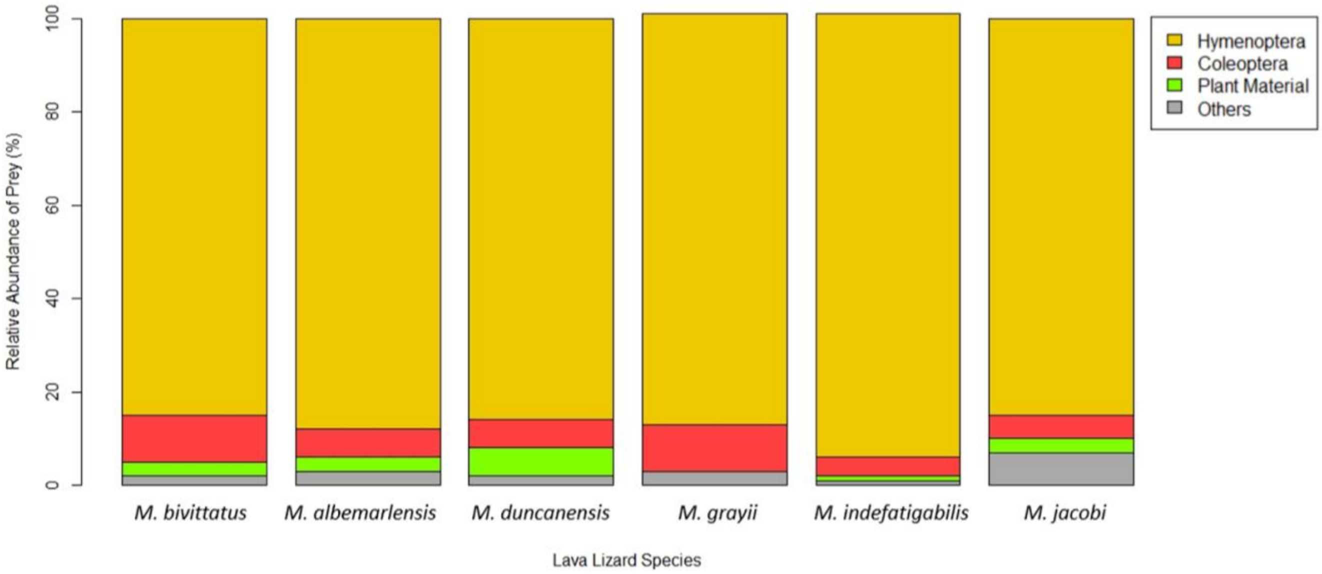

Fig 2. *Relative abundance of prey items consumed by six species of Galápagos lava lizards*

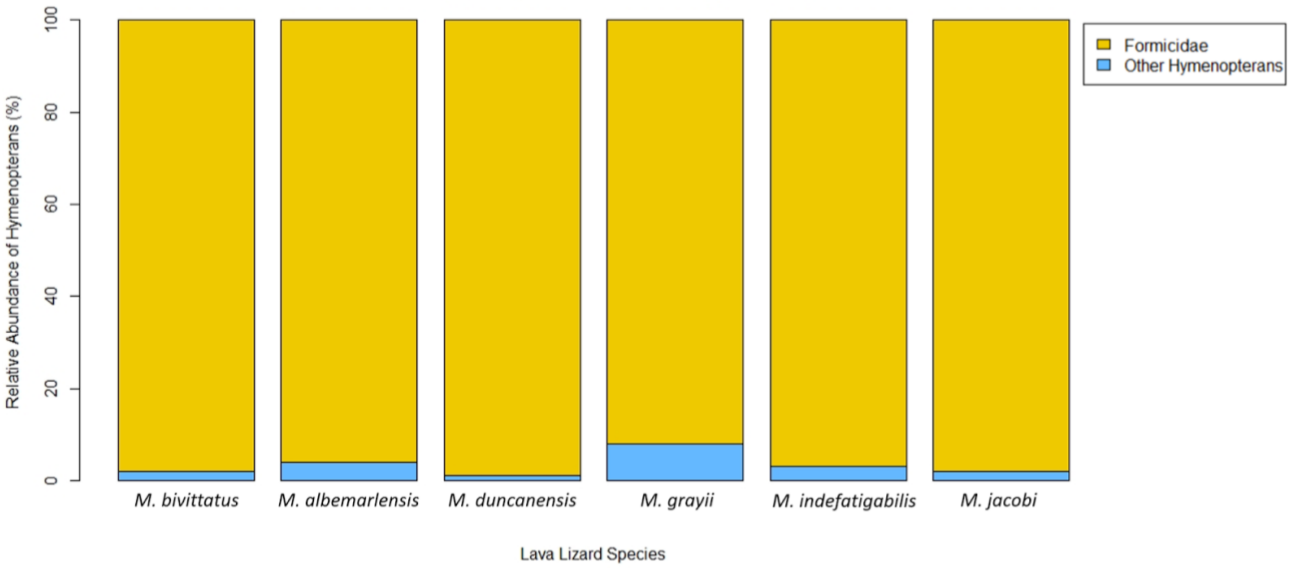

Fig 3. *Relative Abundance of Hymenopterans Concumed by Galápagos Lava Lizards*

Hymenopterans consumed by the six studied Microlophus lava lizards. Ants (Formicidae) represent between 92-99 % of all consumed hymenopterans, whereas the other 1-8% are bees and wasps.

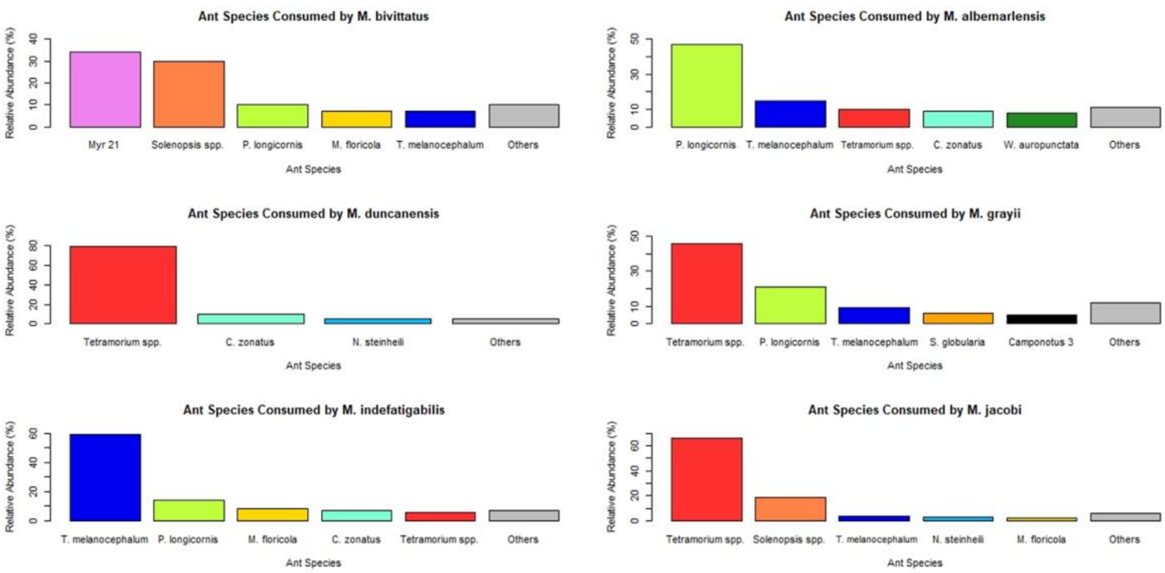

Fig 4. *Most consumed ant species by each of the studied Microlophus Galápagos lava lizards*

From the 18 ant morphospecies registered, two morphospecies (Myr 21 and Myr 22) could not be identified down to the genus level. Myr 21 was a rare species; 60 individuals of Myr 21 were registered for one single fecal sample collected from San Cristóbal island (*Microlophus bivittatus*), making it the most abundant ant species of the San Cristóbal lava lizard *M. bivittatus* (see Fig. 4). On the other hand, Myr 22 was registered from three islands (Isabela, Santa Cruz, and Santiago). Myr 22 could potentially be identified as *Brachymyrmex heeri*, an introduced species in the Archipelago. Further molecular analyzes are needed for correctly identifying both morphospecies.

Additionally, four more ant morphospecies were only identified down to the genus level. One of these species belongs to the *Camponotus* genus. It is likely that the sample corresponds to *C. brettesi*, which is the only species in the *Camponotus* genus registered in the Archipelago besides the other *Camponotus* species listed on ANNEX C and *C. macilentus*, which is notoriously different from *C. brettesi*. Other samples were identified to the genus level (*Cyphomyrmex* spp., *Pheidole* spp., and several *Solenopsis* spp.). Further molecular analyzes are needed for correctly identifying ant species that were only identified to the genus level.

Table 1. *Simpson-Index (B) for prey items and ant prey items found in all six Galápagos lava lizards*

Island	Lizard Species	Overall Simpson Index (B)	Ant Species Simpson Index (B)
San Cristóbal	Microlophus bivittatus	0,72	0,23
Isabela	Microlophus albemarlensis	0,77	0,27
Pinzón	Microlophus duncanensis	0,74	0,64
Floreana	Microlophus grayii	0,77	0,27
Santa Cruz	Microlophus indefatigabilis	0,9	0,38
Santiago	Microlophus jacobi	0,72	0,47

All Galápagos lava lizards show low levels of prey diversity as B values ranged from 0,72 and 0,9. When comparing B’ values of the Galáapagos lava lizards to B’ values reported for other *Microlophus* lizards that inhabit the continent (see Fig. 5) it is evident that the diversity of consumed prey items of Galápagos lava lizards is lower in comparison to prey diversity found on continental *Microlophus*. However, when analyzing the ant species consumed, B values ranged between 0,23 and 0,64 among Galápagos lava lizards (Table 1), which suggests that ant species diversity found on the diets of these lizards is moderate to very high. For this reason, it is proposed that when consuming ant species, Galápagos lava lizards tend to be more generalist and do not show preferences for a particular ant species. In fact, a relative high amount of different ant species were found on the lava lizards. 15 out of the 18 ant species found in fecal samples were consumed by *M. indefatigabilis*, 13 were consumed by *M. jacobi*, 11 were consumed by *M. albemarlensis*, 10 by *M. grayii*, 9 by *M. bivittatus*, and 6 by *M. duncanensis*.

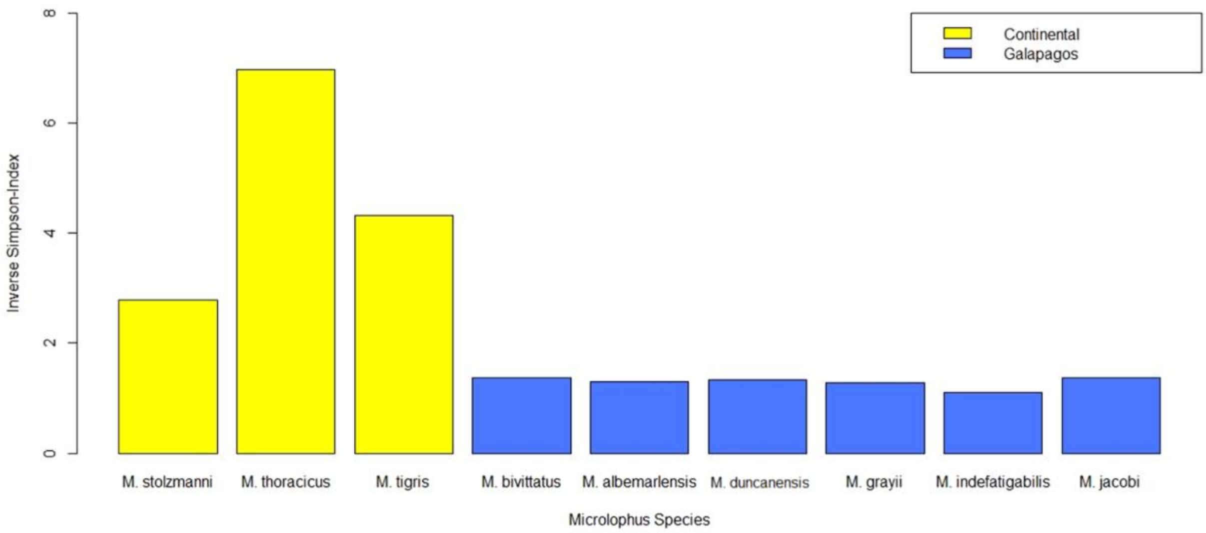

Fig 5. *Comparison of B' values between Microlophus species of the Galápagos and Microlophus species of continental South America*

Also, Table 1 shows that in contrast to overall prey abundance, ant prey abundance found in Galápagos lava lizard diets is relatively high. Most of the Simpson values range from 0,23 and 0,64, indicating high ant diversity found on fecal samples of Galápagos lizards.

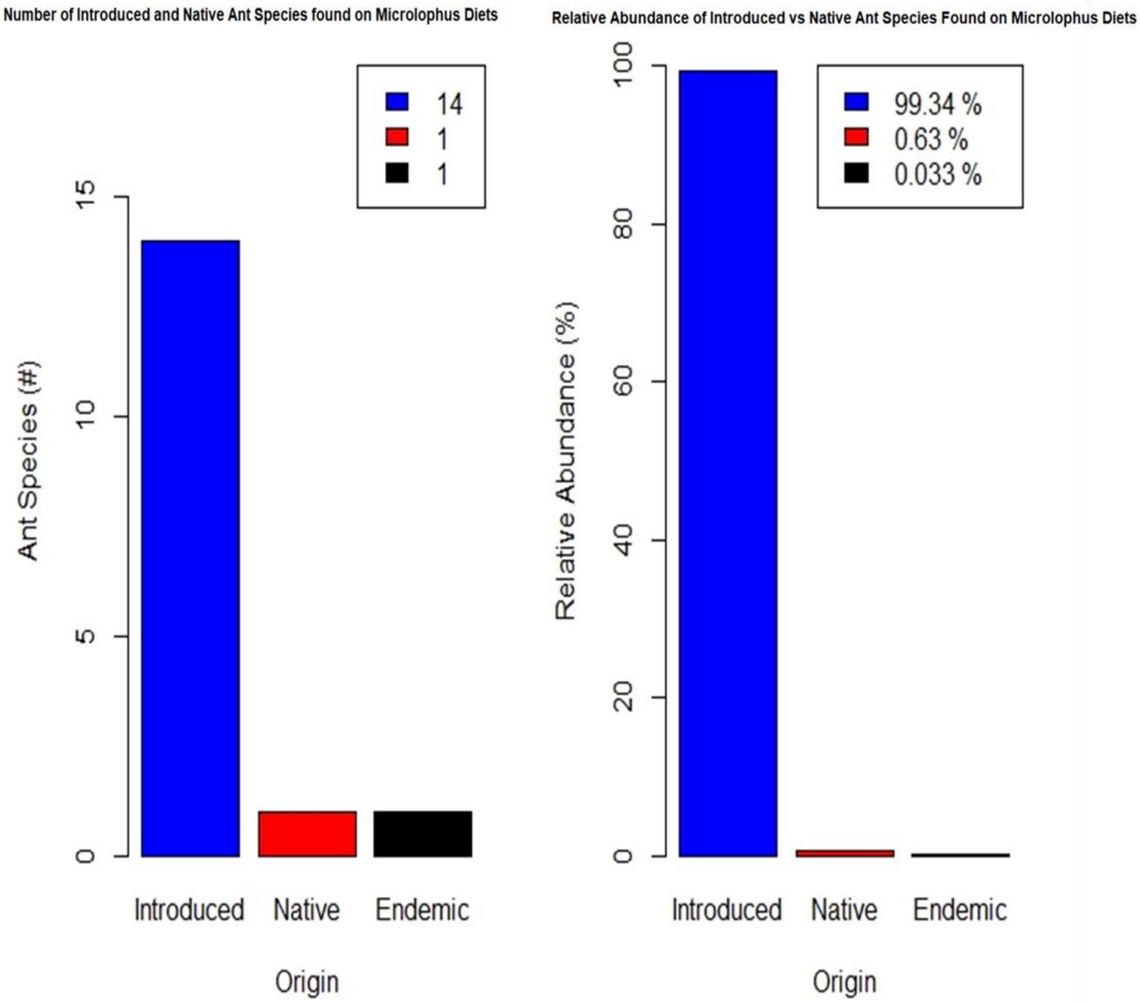

Fig 6. *Comparison of Ant relative abundance and richness vs their ecological status (Introduced vs Native)*

A total of 6068 ant individuals were found on fecal samples from *Microlophus* lizards. From the sixteen ant species that were assigned a proper taxonomic level, it was found that fourteen out of the sixteen ants (87,5 %) were invasive species. One of the remaining ant species was found to be endemic (*Camponotus planus*), and the last ant species (which could not be identified down to the species level, but it is suspected to be *C. brettesi* based on morphological features) was classified as a native species to the Galápagos.

Introduced ants represent the vast majority of the diet (99.34%, 6028 items) consumed by the Galápagos lava lizards. 38 prey items (or 0,63 %) were native ant species (possibly *C. brettesi*) and only 2 items (or 0,033% *C. planus*) were endemic species (*Camponotus planus*).

Also, the San Cristobal and Isabela lava lizards (*M. bivittatus* and *M. albemarlensis* respectively) fed exclusively on introduced ant species. For Pinzon lava lizard, the relative abundance of introduced ant species in their diets was 99 %, and 1 % of endemic species. For Floreana lava lizard, 95 % of consumed ant species were introduced, and 5 % of them were native ants. For the relative abundance of introduced ant species in the diets of Santa Cruz lava lizard, introduced ant species account for 98,98 % of consumed ants, 1 % for native species, and 0,02 % for endemic ant species. For Santiago lava lizard, the relative abundance of introduced ant species in their diets was 99,5 %, and 0,5 % for native species.

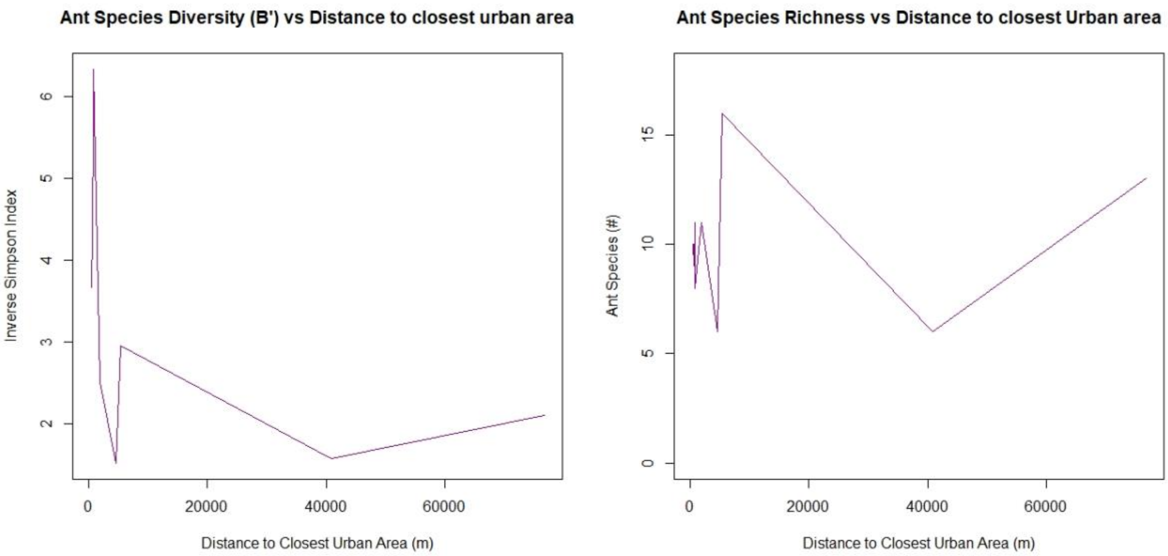

Fig 7. *Distance to closest urban area vs ant species diversity and richness*

When analyzing ant species richness and diversity it can be evidenced that both ant species richness and diversity found on Galápagos lava lizards tend to decrease when sampled sites were further away from a populated area of the Archipelago.

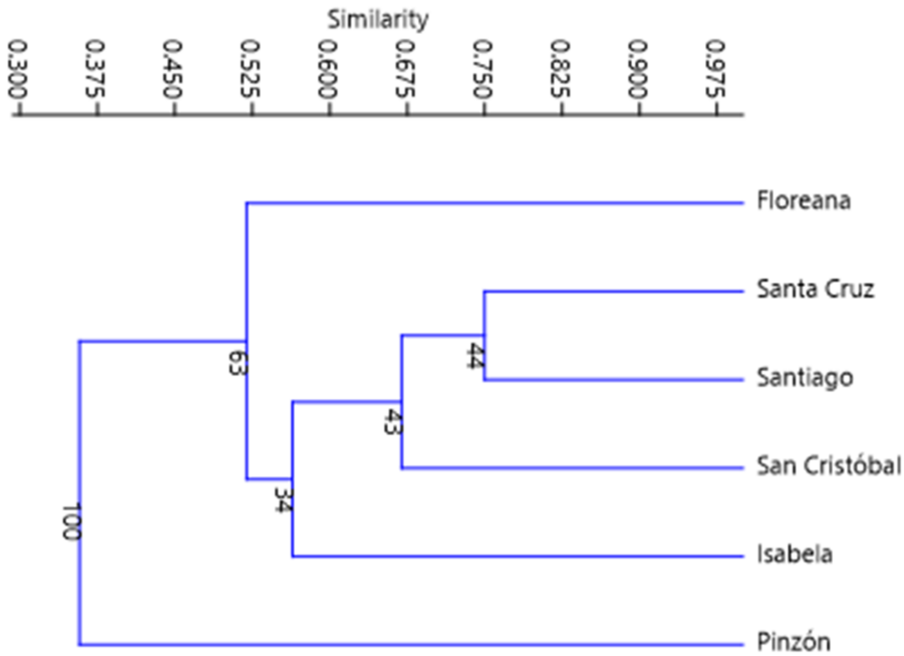

Fig 8. *Level of similarity between ant communities found on all six islands sampled based on Jaccard index*

Additionally, when comparing ant composition of every Lava lizard (every island), it can be seen that the most different ant community of the study is located in Pinzón island. However, the ant community found on Santiago island (which is an inhabited island) shows that it is more similar to the ant community found on Santa Cruz island, rather than Pinzon island.

DISCUSSION

Diet of Galápagos Lava Lizards

The six species of Galápagos *Microlophus* lava lizards heavily depend on hymenopterans (85-95 %), followed by coleopterans (4-10 %), and plant structures (0-6 %) for their diet (Fig. 2). Other invertebrates (e.g., orthopterans, dipterans, hemipterans, mantis, jumping spiders) were rare and scarce in the analyzed feces. A complete list of all consumed prey items by lava lizards can be found on ANNEX B.

The importance of hymenopterans in the diet resembles the results of studies on continental *Microlophus* where the most consumed prey items were also ants. A study on the diet *M. occipitalis*, that inhabits the coast of Ecuador and Peru, found that the most abundant prey items consumed were Hymenoptera (58,9%), Coleoptera (15,2%), and Homoptera (4,3%) (Chávez-Villavicencio et al., 2018). Remarkably, all Hymenoptera consumed by *M. occipitalis* were ants. Also, the study of Beuttner & Koch (2019) on the diet of the Peruvian *Microlophus stolzmanni* found that this lava lizard is a generalist semi-herbivorous reptile that feeds mainly on colony building insects (like ants). A similar study on the also Peruvian *M. thoracicus* found that the main items consumed by this lizard include ants (44,1%), followed by plant material (34,6%) and insect larvae (9,6%) (Pérez et al., 2015).

A perhaps more challenging study relates to *Microlophus peruvianus*; Péfaur & López-Tejeda (1983) found that its diet consisted mainly of adult coleopterans and ants. However, a more recent study reported that the most abundant prey items were amphipods (55,8 %) and coleopterans (17,8 %) (Quispitúpac & Pérez, 2008). The reasons behind these discrepancies may involve the ecology of *M. peruvianus*. In contrast to other *Microlophus* lizards, *M. peruvianus* can be found inhabiting marine intertidal zones, sandy beaches, salt crush beaches, as well as rock walls, and inside houses (Paniura-Palma, 2016; Venegas et al., 2017; Péfaur & López-Tejeda, 1983; Pérez & Lleellish, 2015).

Therefore the diet of both continental and Galápagos species of *Microlophus* lava lizards share a dependance on ants as their main prey. However, in contrast with the continental species, the Galápagos lava lizards depend almost exclusively on ants (Fig. 2 & 3) . Therefore,we propose that all six *Microlophus* lizards of the Galápagos analyzed for this study show a strong tendency towards myrmecophagy, but they can eventually include other items on their diet.

Like other continental *Microlophus* lizards, the Galápagos lava lizards also consume plant material. In fact, plant material is the third most consumed item by all six Galápagos lava lizards studied, suggesting that they are omnivores. As there is no information on the sex and age of the individuals from which the feces were collected from, it is not possible to establish if plant material is consumed indifferently by all age groups and both sexes of *Microlophus* lava lizards, or if plant material is consumed by a specific group age and sex. For example, Hervías-Parejo et al. (2020) reported that Galápagos lava lizards could act as pollinators across the islands. Despite they they collected both males and females, the study does not mention if one sex had a tendency of eating more plant material than the other. Additionally, it has been reported that plant material becomes a more important food resource for *M. stolzmanni* as the individuals mature (Beuttner & Koch, 2019). For instance, it is suggested that adult *Microlophus* lava lizards of the Galápagos could potentially eat more plant material in comparison with juveniles, as this tendency has been observed in several other lizard species (Cooper & Vitt, 2002; Dessem, 1985; van Leeuwen et al., 2011). It has been suggested that juvenile lizards lack the intestinal microflora that allows adult lizards to digest cellulose obtained from plant material (Troyer, 1982). Nevertheless, more work is needed to determine how does plant material consumption of the Galápagos lava lizards varies across groups ages and sex, as well as their ecological role as pollinators and/or seed dispersers.

Differences of diet composition among Galápagos Lava Lizards

The overall prey diversity in five of the six lava lizards (*M. bivittatus, M. albemarlensis, M. jacobi, M. grayii* and *M. duncanensis*) is low, whereas the diversity of prey items in *M. indefatigabilis* (Santa Cruz lava lizard) is very low (see Table 1). Several factors could be attributed as a cause of low levels of diversity in the diets of Galápagos lava lizards. First, it is possible that the Galápagos *Microlophus* lava lizards have adapted their foraging strategies towards ants. Given that invertebrate diversity on oceanic islands is relatively low (Kier et al., 2009), adapting to readily available prey makes evolutionary sense. For this reason, it is possible that lava lizards of the Archipelago specialize in hunting and feeding on the most abundant prey available in the environment, which, in this case, could be ants.

Another reason why there is low diversity in prey consumption by these lizards could be because of the presence and abundance of introduced ant species. It is known that one of the biggest threats that the Galápagos' Archipelago has nowadays is the presence of invasive species (Cayot et al., 2021). Invasive species are a huge threat not only in Galápagos, but also in the world as invasive species can displace native populations (Huxel, 1999). In fact, the best documented effects of invasive insects has been reported in invasive ant species (Kenis et al., 2008), which are the most abundant prey item found on *Microlophus* lava lizards of the Galápagos (Fig. 3).

The diet of *M. indefatigabilis* (Santa Cruz' lava lizard) has significant variations when compared to the diets of the other Galápagos lava lizards. The overall prey diversity found on *M. indefatigabilis* had an overall B value of 0,90, which suggests that there are very low levels of diversity of prey items consumed by Santa Cruz' lava lizard. Additionally, it was previously stated that when taken into consideration the six *Microlophus* species analyzed, the most consumed species was *T. melanocephalum*, having a relative abundance of 44%. However, this percentage is influenced by the exorbitant abundance of *T. melanocephalum* found in fecal samples from *M. indefatigabilis*. From the 2677 *T. melanocephalum* individuals registered from fecal samples from all six species of lizards, 2536 individuals (95%) were from the Santa Cruz' lava lizard. Additionally, despite showing low levels of diversity (Simpson index; Table 1), this lava lizard consumed prey from 11 different insect/invertebrate orders and 15 distinct ant species.

The diet differences of *M. indefatigabilis* could be explained by the island in which this lava lizard inhabits: Santa Cruz. This island is the most populated island of the Galápagos, as well as one of the most touristic islands of the Archipelago (Burbano et al., 2022). It is possible that human presence has facilitated multiple arrivals and the establishment of invasive ants in Santa Cruz. For example, it has been documented that Pacific Islands are the major receptors of introduced ant species on a global scale (McGlynn, 1999).

When comparing overall prey diversity between Galápagos lava lizards and continental *Microlophus* species it has been found that none of the B' values for Galápagos lava lizards reach more than 1.40, whereas B' values for continental *Microlophus* species range between 2.79 to 6.97 (Fig. 5). These results suggest that, in comparison with continental species, the *Microlophus* species of the Galápagos exhibit low levels of prey diversity in their diets, which means that they are not generalist lizards in comparison with their continental counterparts. However, this could also be attributed to low levels of overall invertebrate diversity in comparison with the continent. Based on these results (see Fig. 2 and Fig. 3) it is proposed that Galápagos lava lizards are mainly myrmecophagous but they will opportunistically consume other prey items.

Ant species diversity

Ants make up to 89% of all prey consumed by Galápagos lava lizards. Ant species are considered as ecologically diverse insects (Guénard, 2013), as they can become keystone species in several ecosystems by supporting a vast amount of different taxa in a direct or indirect way (Parker & Kronauer, 2021). Our study shows that ants are crucial for the survival of *Microlophus* lava lizards as they are their main source of food. A total of eighteen different ant species were identified on the six *Microlophus* lava lizards' fecal samples (see ANNEX C). From the ant species that were identified down to the genus or species level, 11 of them (69%) are introduced species, 3 of them (19%) are potentially introduced species, and 2 of them (12%) are native species. This means that potentially, 88% of all ant species found on fecal samples from Galápagos lava lizards are introduced (Fig. 6). Thus, we can speculate that the introduced ant species may have produced an increase of food items for the Galápagos lava lizards. However, we note that there is no information about the population density of native ants and how that has changed with the arrival of introduced ants.

One important thing to note is that *Tetramorium* spp. are the most preyed ant species on both of the inhabited islands sampled for this study (Santiago and Pinzón) as well as the least inhabited island of the Archipelago, which is Floreana island with an estimate of 130 inhabitants. Relative abundance of *Tetramorium* spp. found on fecal samples of Galápagos lava lizards of Floreana, Santiago, and Pinzón Island account for 46 %, 66 %, and 79 % respectively.

In contrast, *Tetramorium* ant species found on the diets of lava lizards that inhabit the most populated islands (Santa Cruz, San Cristóbal, and Isabela) are very scarce and rare as they account for less than 10 % of all ant species consumed. The *Tetramorium* spp. complex of the Galápagos islands includes five different ant species, all of them introduced in the Archipelago. These species include: *T. caldarium*, *T. bicarinatum*, *T. lanuginosum*, and *T. simillimum*

(AntWeb, 2022; Herrera et al., 2014; *T. lucayanum* is excluded from the *Tetramorium* spp. complex as this was the only *Tetramorium* species that could be identified down to the species level for this study). Galápagos lava lizards that inhabit unpopulated islands of the Archipelago such as Santiago and Pinzón Island could be foraging more on *Tetramorium* ant species as it has been reported that several *Tetramorium* species are moderately aggressive and they are not as aggressive as other ant species (Astruc et al., 2001). This suggests that *Tetramorium* species would be able to thrive in environments with reduced levels of competition with other ant species because other introduced ant species tend to displace many native (an non-native) ant species as they are highly aggressive and dominant (Bertelsmeier et al., 2015). For example, it has been reported that in urbanized areas, human activities can create a diverse range of habitats for ant communities that range from gardens and parks, to residential and industrial areas which facilitates the existence and distribution of dominant ant species (Sarty et al., 2006). Also, invasive ant species tend to be highly abundant and dominant in urbanized areas as they are able to tolerate a wider range of environments, are able to exploit resources in a more effective way, and are more aggressive and competitive when compared to native species (Stringer et al., 2009; Pacheco & Vasconcelos, 2007). With the lack of urbanized areas, it is possible that the *Tetramorium* species are one of the most dominant species in unpopulated islands, which is reflected on the ant consumption by the Floreana, Pinzon, and Santiago lava lizards. For example, it has been suggested that *T. lucayanum* is relatively common in tropical islands (such as Madagascar and the Samoa and Galápagos islands) due to the reduction in competition towards dominant ant species in these habitats (Wetterer, 2011). In a similar way, it has been reported that despite both *T. caldarium* and *T. simillimum* are tramp ant species distributed over the world, they do not seem to have any important ecological impacts given that they are not as aggressive or dominant as other introduced ant species (Wetterer & García, 2015). However, a study with *T. bicarinatum* showed that workers of this ant species show a lack of intraspecific competition, but they do show aggressive behaviors towards other ant species (Astruc et al., 2001), which suggests that despite the *Tetramorium* spp. complex of the Galápagos might not do well against other introduced species in urbanized environments, they are still one of the most dominant ant species in non-urbanized islands. Also, this could be related to the low levels of both ant diversity and richness seen in the places that are farthest from urbanized areas (Fig. 7). With the lack of anthopogenic influence, *Tetramorium* ant species are able to thrive in less competitive environments in which they become highly abundant as seen on Santiago, Pinzón and Floreana islands. Therefore, the further away from a populated area, the more likely to see moderately introduced species (such as *Tetramorium* spp.) dominating over other ant species.

In contrast, the most abundant ant species on the diets of the Galápagos lava lizards that inhabit the most populated islands (Santa Cruz, San Cristóbal, and Isabela) include *T. melanocephalum*, *P. longicornis*, *M. floricola*, *C. zonatus*, and *Solenopsis* spp.

T. melanocephalum, also known as the ghost ant, is classified as an introduced ant species in the Galápagos that is considered a pest in tropical and subtropical regions and is becoming more common in temperate areas (Wetterer, 2008). This ant species is known for being able to adapt to a wide variety of habitats as well as being capable of building its nests in different substrates such as soil, under rocks, tree bark and fallen trees (Nickerson et al., 1969). It has been found that the ghost ant is the most prevalent ant in Brazilian hospitals, and it has the higher potential to become a vector for pathogens (Moreira et al., 2005). Also, it has been evidenced that *T. melanocephalum* is usually associated with disturbed areas, but it has also been reported in several natural areas like for example in different Galápagos islands (Aesch, 2006). In a similar way, *P. longicornis*, also known as the longhorn crazy ant, is another highly invasive ant species that is mainly distributed in tropical and subtropical regions of the world, and it is usually found on disturbed areas, but it can also thrive in undisturbed areas (Wetter, 2008). It has been reported that *P. longicornis* is a highly cooperative ant species that has a polydomic nesting strategy (Wetterer, 2008). In fact, the longhorn crazy ant is nowadays considered as one of the top seven most invasive ant species of the world (Bertelsmeier et al., 2015). Also, *Solenopsis* fire ants, specially *S. geminata* (which was registered in the diets of some of the Galápagos lava lizards) is considered as a very aggressive ant, and it is well documented that due to its ferocious predation on arthropod communities, *S. geminata* possess huge threats in the decline of arthropod populations (Wauters et al., 2018). In fact, it has been seen that *S. geminata* has serious effects on declines on vertebrate clutches in the Galápagos as it has been reported that this ant has implications on the nesting behavior of land tortoises and iguanas (Roque-Albelo & Causton, 1999).

When comparing ant communities found on each of the Galápagos lizard diets it can be seen that in fact, Pinzón island shows the most different ant community composition when compared to the other islands (Fig. 8). This is an expected result as Pinzón island is the only island in the Archipelago that hasn't been colonized by humans, so in theory this island should have the least anthropogenic effects on ant populations in comparison with the other islands studied. Also, it was evidenced that *Tetramorium* species are highly dominant in Pinzón island (relative abundance of 79 %), and overall ant diversity in this island is the lowest when compared to the other islands studied (see Table 1). However, it was expected to see a similar ant composition between all three major populated islands (Santa Cruz, Isabela, and San Cristóbal). Instead, as seen on Figure 8, it appears that the ant community found on Santiago island is more similar to the Santa Cruz ant community, rather than the ant communities between San Cristóbal, Isabela, and Santa Cruz. This could be attributed to similar ant communities established on both Santiago and Santa Cruz islands (see ANNEX A). Also, despite the Santiago lava lizard feeds mostly on *Tetramorium* ants, the diet of this lizard showed the highest consumption of ant species along with the Santa Cruz lava lizard (13 and 15 ant species consumed respectively). For this reasons, it is possible that the ant communities found on Santiago island are more similar with the ant communities found on Santa Cruz island.

As mentioned earlier, the B values obtained for ant prey diversity suggest that when consuming ant species, Galápagos lava lizards tend to be more generalists and they might not specialize at hunting a specific group of ants. However, it was evidenced that some ant species (such as *T. melanocephalum*, *Tetramorium* spp., and *P. longicornis*) can become extremely abundant and account for more than 60 % of all consumed ant species depending on the Galápagos lava lizard analyzed. For these cases, it is suggested that there is not a preference of the consumption of these ant species by Galápagos lava lizards. Instead, given their ecological and biological characteristics (such as having polygynous and/or polydomic colonies, showing no intraspecific aggression and strong interspecific aggression, and the ability to use resources in a more efficient way), some introduced ant species in the Archipelago (*T. melanocephalum*, *P. longicornis*, *M. floricola*, *Tetramorium* spp., etc.) are considerably more abundant than other ant species, reason why the Galápagos lava lizards might be consuming some ant species more than others.

The lowest ant prey diversity was registered in the two unpopulated islands of the study: Santiago and Pinzón. B values for Santiago and Pinzon were of 0,47 and 0,64 respectively. Moderate levels of ant prey diversity in these islands can be explained by the lack of anthropogenic influence in comparison to populated islands such as Santa Cruz, San Cristóbal and Isabela. Instead, the highest ant prey diversity was recorded for San Cristóbal and Isabela, with B values of 0,23 and 0,27 respectively. This shows a tendency of seeing very high ant prey diversity levels in populated and touristic islands, whereas unpopulated areas with less anthropogenic effects such as Santiago and Pinzón exhibit lower and moderate levels of ant prey diversity. This could happen due to urbanization as it has been seen that human populated areas tend to increase the availability of food in both terrestrial and aquatic systems (El-Sabaawi, 2018) which some introduced and invasive species can take advantage of and increase their abundance (Santana et al., 2020). By having no settled human populations, environmental disturbances on both Santiago and Pinzón islands are very low, so there are no food inputs from human origin as seen on urbanized islands. Therefore, despite registering introduced ant species, the relative abundance of ant prey consumption in Santiago and Pinzón islands is the lowest when compared to the other four islands sampled for this study.

Besides the consumption of introduced ant species, plastic threads were also found on fecal samples of three lava lizards. Plastic threads were found on one fecal sample from the Floreana lava lizard (*M. grayii*), and on two fecal samples from the Isabela lava lizard (*M. albemarlensis*). The most plastic threads were found on the Santa Cruz lava lizard (*M. indefatigabilis*), as seven fecal samples from this lizard contained this item. Three of these fecal samples were collected from El Garrapatero, and the remaining four were collected from Tortuga Bay. The finding of plastic threads in fecal samples of three species of Galápagos lizards is a clear indicator of direct impacts of human activity in the Archipelago. The most plastic threads registered per fecal sample is in Santa Cruz, which is the most populated and touristic island of the Archipelago. However, Floreana, which accounts for a population of around 130 inhabitants also registered one plastic thread in one fecal sample, which suggests that anthropogenic impacts in the Archipelago are not restricted to the "big" populated and touristic islands, but they are also having effects on less populated and crowded islands.

Ecological implications of ant species consumed by lava lizards

The vast majority of ants consumed by *Microlophus* lizards are introduced species (99,34 %). However, it is important to distinguish that *Microlophus* lizards of the Galápagos might not be specialists at hunting introduced ant species. Instead, it is suggested that *Microlophus* lizards of the Galápagos might be ant generalists that feed on the most abundant group that is available, which in this case, they are invasive ant species. The reason why this is plausible is because in comparison to native species, invasive ant species are more aggressive and highly competitive and dominant species that tend to displace native ant species (Bertelsmeier et al., 2015).

One interesting finding of this study is that the most abundant *Camponotus* species consumed by lava lizards was *C. zonatus*, which was the fourth most consumed ant species by lava lizards (relative abundance of 6 % of ant prey items). What's interesting about this species is that workers from *C. zonatus* are active during the night (Herrera & Causton, 2010). There has not been any reports of *Microlophus* lava lizards of the Galápagos exhibiting nocturnal foraging behaviors. Therefore, the finding of this ant in the guts of all six Galápagos lava lizards can mean two things. First, the finding of *C. zonatus* on fecal samples could potentially mean that lava lizards of the Galápagos actively search for nests of this ant species during the day, or it could also mean that Galápagos lava lizards might be active during night and forage on *C. zonatus*.

Also, several fecal samples collected in Santa Cruz contained between 300 and 600 ant individuals belonging to the same ant species (*T. melanocephalum*). It is known that *T. melanocephalum* ants build polygynous colonies that can range between 100 and 1000 individuals (Harada, 1990). These findings suggested that it is possible that the Santa Cruz lava lizard (and possibly the other lava lizards studied) might be active foragers of the most abundant group of ant species given the large numbers of ant individuals found on some fecal samples.

It is crucial to study more in detail foraging behaviors of *Microlophus* lizards to determine if they actively search for prey.

Limitations

Prey items were identified using microscopy methods, and the identification of the occurrence of one organism was based on the presence of a head. It is plausible that several prey items might have been completely digested by the lizard's gut, so they were impossible to report through microscopy. Additionally, prey items should be analyzed using DNA sequencing, even at the level of order identification as microscopy identification methods of prey items can not be precise (Pereira et al., 2019).

Given the methodology used for sampling feces from lava lizards, it is unknown if they come from a male, female, juvenile or adult individual. It is also unknown if all fecal samples come from lava lizards. Therefore, more standardized methods should be applied for identifying physical characteristics of the individual lava lizards that are sampled.

As mentioned earlier, some islands were oversampled whereas others were undersampled. For future studies, it is important to have the same amount of sampling effort for every island for assuring that the differences in diet consumption between Galápagos lava lizards is related to the differences in the ecology of lava lizards and prey abundance, and not to sampling effort.

Also, sampling only occurred between December and January, which corresponds to the transition between the dry and wet seasons in the Archipelago (Lack, 2008). More sampling should be carried out during different times of the year, as invertebrate communities in the Archipelago could be shifting due to seasonal variations in the Galápagos.

CONCLUSIONS

This study provides first insights of the diets of six *Microlophus* lava lizards of the Galápagos islands.We found that ants make up most of the diets of all lizards studied, followed by coleopterans and plant material. No vertebrate prey items (such as tails of conspecifics or geckos reported by Moore et al., 2017) were found on fecal samples analyzed.

All of the Galápagos lava lizards studied consumed almost exclusively introduced ant species. However, we suggest that lava lizards are not specifically targeting introduced ants, but that they feed on them opportunistically, and the abundance of their diets might mirror the natural abundances in the environment. The effect of introduced ants in the Galápagos is, for most species, negative; however, the Galápagos lava lizards may actually benefit from a more abundant food item, although the ecological interactions between introduced ants and lizard eggs or juveniles is unknown.

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ANNEX A

List of introduced ant species in the Galápagos islands. Data obtained from (Causton et al., 2006), (Herrera, 2013) & (Herrera et al., 2013).

Ant species	**Galápagos Distribution**
Adelomyrmex myops	Isabela
Brachymyrmex heeri	Isabela, San Cristóbal, Santa Cruz
Brachymyrmex patagonicus	Isabela, San Cristóbal, Santa Cruz
Camponotus zonatus	Floreana, Isabela, Marchena, Pinta, San Cristóbal, Santa Cruz, Santiago
Cardiocondyla emeryi	Floreana, Genovesa, Isabela, Marchena, Pinta, San Cristóbal, Santa Cruz, Santiago, Wolf
Cardiocondyla minutior	Fernandina, Floreana, Isabela, Marchena, Pinta, San Cristóbal, Santa Cruz, Santiago, Wolf
Cardiocondyla nuda	Santa Cruz
Cylindromyrmex whymperi	Isabela, Santa Cruz
Cyphomyrmex rimosus	Isabela, San Cristóbal, Santa Cruz
Hypoponera opaciceps	Fernandina, Isabela, Santa Cruz
Hypoponera punctatissima	Santa Cruz
Monomorium destructor	Floreana, Santa Cruz
Monomorium floricola	Española, Fernandina, Floreana, Genovesa, Isabela, Marchena, Pinta, San Cristóbal, Santa Cruz, Santiago
Nylanderia steinheili	Floreana, Isabela, Santa Cruz, San Cristóbal
Nylanderia vaga	Santa Cruz
Odontomachus bauri	Floreana, Isabela, Santa Cruz, San Cristóbal
Odontomachus ruginodis	Santa Cruz
Paratrechina longicornis	Española, Floreana, Isabela, San Cristóbal, Santa Cruz
Pheidole megacephala	San Cristóbal, Santa Cruz
Pheidole flavens	Isabela, San Cristóbal, Santa Cruz
Pyramica membranifera	Santa Cruz
Rogeria curvipubens	Isabela, Santa Cruz
Solenopsis geminata	Floreana, Isabela, San Cristóbal, Santa Cruz
Solenopsis globularia	Española, Fernandina, Floreana, Genovesa, Isabela, Pinta, San Cristóbal, Santa Cruz, Santiago
Strumigenys emmae	Floreana, Isabela
Strumigenys louisianae	Floreana, Isabela, San Cristóbal, Santa Cruz
Tapinoma melanocephalum	Fernandina, Floreana, Isabela, Marchena, Pinta, San Cristóbal, Santa Cruz, Santiago
Tetramorium bicarinatum	Española, Fernandina, Floreana, Genovesa, Isabela, San Cristóbal, Santa Cruz, Santiago
Tetramorium caldarium	Floreana
Tetramorium lanuginosum	Floreana, San Cristóbal, Santa Cruz, Wolf
Tetramorium lucayanum	Isabela

Tetramorium simillimum	Española, Floreana, Isabela, San Cristóbal, Santa Cruz, Santiago
Wasmannia auropunctata	Española, Floreana, Isabela, Marchena, San Cristóbal, Santa Cruz, Santiago

ANNEX B

Consumed prey by Galápagos lava lizards.

Galápagos Lava Lizard Species	Island	Hymenoptera	Coleoptera	Hemiptera	Odonata	Blattodea	Orthoptera	Diptera	Psocodea	Salticidae	Lepidoptera	Psocoptera	Mantodea	Acari	Skin Moult	Plant Structure	TOTAL
Microlophus bivittatus	San Cristóbal	177	21	3	0	0	0	0	0	0	0	1	0	0	0	7	209
Microlophus albemarlensis	Isabela	570	42	3	0	1	1	2	0	0	13	0	0	0	0	19	651
Microlophus duncanensis	Pinzón	187	14	3	0	0	0	1	0	0	0	0	0	0	0	13	218
Microlophus grayii	Floreana	238	27	4	0	0	2	0	1	0	0	0	0	0	0	0	272
Microlophus indefatigabilis	Santa Cruz	4463	176	26	11	1	0	1	0	1	1	0	1	1	0	19	4701
Microlophus jacobi	Santiago	632	36	24	0	0	5	10	1	1	8	1	0	0	2	25	745

ANNEX C

Ant species consumed by Galápagos lava lizards.

Ant Species	Status	Relative Abundance (#)	Island	Observations
Camponotus 3	Native	38	Floreana, Santa Cruz, Santiago	Possibly *C. brettesi*
Camponotus planus	Endemic	2	Pinzón, Santa Cruz	
Camponotus zonatus	Introduced	398	Floreana, Isabela, Pinzón, Santa Cruz, San Cristóbal, Santiago	
Cyphomyrmex spp.	Introduced or Native	1	Santa Cruz	
Monomorium floricola	Introduced	385	Floreana, Isabela, Pinzón, Santa Cruz, San Cristóbal, Santiago	
Nylanderia steinheili	Introduced	83	Floreana, Pinzón, San Cristóbal, Santa Cruz, Santiago	
Odontomachus bauri	Introduced	101	Isabela, San Cristóbal, Santa Cruz	
Paratrechina longicornis	Introduced	920	Floreana, Isabela, San Cristóbal, Santa Cruz, Santiago	
Pheidole spp.	Introduced or Native	1	Isabela	
Solenopsis spp.	Introduced or Native	258	Floreana, Isabela, San Cristóbal, Santa Cruz, Santiago	Most individuals possibly *S. geminata*
Solenopsis geminata	Introduced	37	Floreana, Pinzón, San Cristóbal, Santa Cruz, Santiago	
Solenopsis globularia	Introduced	26	Floreana, Isabela, Santa Cruz, Santiago	

Tapinoma melanocephalum	Introduced	2677	Floreana, Isabela, San Cristóbal, Santa Cruz, Santiago	95 % of individuals were found on Santa Cruz
Tetramorium lucayanum	Introduced	6	Santiago	
Tetramorium spp.	Introduced	977	Floreana, Isabela, Pinzón, Santa Cruz, Santiago	
Wasmannia auropunctata	Introduced	50	Isabela, Santa Cruz, Santiago	84 % of individuals were found on Isabela
Myr 21	Unknown	60	San Cristóbal	All 60 individuals were found in one single fecal sample
Myr 22	Unknown	48	Isabela, Santa Cruz, Santiago	Possibly *Brachymyrmex heeri*