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Aliens on the Menu: High Prevalence of Introduced Ants in the Diet of Galápagos Lava Lizards, *Microlophus* spp.

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Abstract:

The Galápagos Archipelago, a unique and ever-changing natural experiment, has seen an increase in introduced species due to increased human mobility. Among these, introduced ants represent a significant concern given their potential to reach high densities and displace native fauna. This study analyzed the diet of six Galápagos lava lizard species (*Microlophus* spp.) through the examination of 177 fecal pellets collected over two seasons. We identified 7084 food items across 39 categories, with ants predominating, making up 65% of occurrences and 90% of the total abundance. Notably, introduced ants constituted 57.1% of these occurrences and 79.4% of the total abundance, indicating a significant prevalence of non-native prey. This finding suggests a substantial shift in the islands' ecological dynamics away from their natural state (i.e., without introduced ants). We also explore the dietary breadth of each lizard species and their similarity. Finally, we discuss the possible direct and indirect effects of the high prevalence of ants in the diet of Galápagos lava lizards, report interesting findings in their diet, and advocate for the use of feces as a non-invasive method to monitor for invasive ants. Our study highlights the ecological changes underway on these islands, underscoring the need for targeted conservation strategies to mitigate the impact of invasive species and preserve Galápagos biodiversity.

Keywords: Archipelago, exotic, Formicidae, island, invasive, Tropicuridae.

Resumen:

El archipiélago de Galápagos, un experimento natural único y en constante cambio, ha experimentado un aumento en las especies introducidas debido a la mayor movilidad humana. Entre estas, las hormigas introducidas representan una preocupación significativa dado su potencial para alcanzar altas densidades y desplazar la fauna nativa. Este estudio analizó la dieta de seis especies de lagartijas de lava de Galápagos (*Microlophus* spp.) mediante el examen de 177 pellets fecales recolectadas durante dos temporadas. Identificamos 7084 ítems alimenticios

en 39 categorías, predominando las hormigas, que constituyeron el 65% de las ocurrencias y el 90% de la abundancia total. Notablemente, las hormigas introducidas constituyeron el 57.1% de estas ocurrencias y el 79.4% de la abundancia total, lo que indica una prevalencia significativa de presas no nativas. Este hallazgo sugiere un cambio sustancial en la dinámica ecológica de las islas, alejándose de su estado natural (es decir, sin hormigas introducidas). También exploramos la amplitud de la dieta de cada especie de lagartija y su similitud. Finalmente, discutimos los posibles efectos directos e indirectos de la alta prevalencia de hormigas en la dieta de las lagartijas de lava de Galápagos, presentamos hallazgos interesantes en su dieta y abogamos por el uso de heces como un método no invasivo para monitorear hormigas invasoras. Nuestro estudio destaca los cambios ecológicos en curso en estas islas, subrayando la necesidad de implementar estrategias de conservación dirigidas para mitigar el impacto de las especies invasoras y preservar la biodiversidad de Galápagos.

Introduction

Island ecosystems, such as the Galápagos Archipelago, are unique laboratories of evolution, harboring numerous endemic species adapted to isolated environments (Peck et al., 2006). However, their isolation makes them susceptible to external threats, particularly introduced species (Toral-Granda et al., 2017). These species, whether intentionally or accidentally introduced, can disrupt the ecological dynamics of endemic flora and fauna (Causton et al. 2006). In the case of introduced ant species, the displacement of local fauna is a well-documented consequence (Lach and Hooper-Bùi 2010; Naughton et al. 2020), but indirect impacts have also been observed (Allen et al. 2004). For instance, the introduction of the fire ant *Solenopsis invicta* in Texas resulted in the displacement of harvester ants (genus *Pogonomyrmex*), the main prey of the Texas horned lizard (*Phrynosoma cornutum*), and potentially contributed to its geographic range reduction (Allen et al. 2004). In California, the introduction of the Argentine ant (*Linepithema humile*) was experimentally shown to reduce hatchling growth rates in coastal horned lizards (*P. coronatum*) through a shift in the prey composition of the lizards living in invaded areas (Suarez and Case 2002). As such, the potential for introduced species to alter these delicate ecological balances and drive native species to extinction is a pressing conservation challenge.

The onset of human colonization in the 17th century, along with the rise in human settlements and tourism in the 20th century, intensified human-related disturbances in the Galápagos archipelago (Stahl, P.W. et al. 2020). The subsequent demographic expansion and intensified human activities in the following decades have adversely impacted various native species, such as blue-footed boobies (Burger and Gochfeld 1993), Darwin finches (Zylberberg et al. 2013), and marine iguanas (French et al. 2010). For native lava lizards (*Microlophus* spp.), specifically, human-made infrastructures (i.e. roads) have resulted in significant fatalities (Tanner and Perry 2007; Medrano-Vizcaíno et al. 2023) and, increased tourism-related activities and urbanization have impacted their behavior and activity patterns, particularly on highly populated islands (Boada-Viteri 2021). Additionally, the introduction of exotic species has escalated over the last decades (Quiroga, D. 2018), particularly regarding small invertebrates (Toral-Granda et al. 2017), including ants (Herrera 2014; Herrera et al. 2020; Herrera et al. 2024) another potential threat to the unique species that inhabit the Archipelago. However, the ecological consequences of introduced species, particularly insects, on lava lizard populations remain unexplored.

Ants, as invasive insects, are notorious for their potential to displace native species and disrupt the ecological equilibrium (Holway et al. 2002; Arnan et al. 2018). Over 200 introduced ant species have established colonies outside their native habitats, with several listed among the world's most noxious invasive alien species (Lowe et al. 2004; Bertelsmeier et al. 2017; Ujijama and Tsuji 2018). With the continued growth of international trade and globalization, the number of invasive ant species continues to rise (Bertelsmeier et al. 2017), as observed on different oceanic islands (e.g., Canary Islands, Hernández-Teixidor et al. 2020; Lang Tengah Island, Gan et al. 2022; Mayotte Island, Hoffmann et al. 2023). The Galápagos islands host a total of 52 ant species, of which 36 are considered introduced (AntWeb, 2024; Herrera et al. 2020; 2024) (Table S1). At least three of those (*Wasmannia auropunctata*, *Solenopsis geminata*, and *Pheidole megacephala*) have been linked to adverse impacts on native biota and are categorized as invasive (Causton et al. 2006; Herrera et al. 2013). For instance, *W. auropunctata* has caused reductions in native invertebrate biodiversity (Clark et al. 1982) and negative effects on nesting giant tortoises (Lubin 1985; Wauters et al. 2018). In regions like New Caledonia, introduced ant species have already precipitated declines in native lizard populations (Jourdan et al. 2001). Yet,

the influence of introduced ant species on Galápagos lava lizards, especially concerning their diet, remains unknown.

In the South American mainland, the dietary habits of *Microlophus* species are well-documented. Research focusing on *M. occipitalis*, *M. stolzmanni*, and *M. thoracicus* have consistently reported a primary reliance on ants as the most important food item (Pérez Z et al. 2015; Chávez-Villavicencio et al. 2018; Beuttner and Koch 2019). Similarly, in the Galápagos Archipelago, lava lizard species display insect-based diets, with sporadic ingestion of other arthropods, small vertebrates (including conspecifics), and varied plant material (Denburgh and Slevin 1913; Stebbins et al. 1967; Hervías-Parejo et al. 2020). Recent observations on the diets of *M. bivittatus* and *M. indefatigabilis* have also revealed, akin to their mainland counterparts, the presence of ants on their diets, supplemented by arthropods and plant material (Lewbart et al. 2017; Moore et al. 2017). Nonetheless, the ant species found have not been determined and, a comprehensive understanding of their relative importance remains to be established.

The ecological impact of introduced ants on native lizards in oceanic islands remains largely unexplored. Elsewhere, myrmecophagous lizards, such as horned lizards, often avoid feeding on introduced ant species (Suarez et al. 2000; Ramakrishnan et al. 2018) or shift their habitats to avoid invaded areas (Webb and Henke 2003). In the case of the Galápagos Islands, understanding the ecological interactions of native species with introduced ants is imperative for its conservation, especially for myrmecophagous lizards that have key ecological roles such as insect population control, prey for other species (Denburgh and Slevin 1913; Stebbins et al. 1967; Snell et al. 1988), and pollinators and seed dispersers (Hervías-Parejo et al. 2019; Hervías-Parejo et al. 2020). Here, we analyzed fecal pellets from six allopatric lava lizard species (*Microlophus* spp.), to test if, like their mainland counterparts, ants are a significant component of their diet and the frequency of introduced ant species in the diet of each species. We further discuss the potential direct and indirect ecological impacts of introduced ants on the ecology and conservation of these lizards.

Methods

Study species

The genus *Microlophus*, also known as lava lizards, includes 23 species distributed along the South-American Pacific coast from northern Peru to north-central Chile (Torres-Carvajal 2024). Ten of these are endemic to the Galápagos Archipelago and evolved under allopatric conditions after two distinct colonization events, forming two clades (Benavides et al. 2007; Benavides et al. 2009). Currently, lava lizard species are distributed across all major islands, with their habitats ranging from the 18 Km² Pinzón Island (*M. duncanensis*) to the larger 4588 Km² Isabela Island (*M. albemarlensis*), and their surrounding islets. Notably, *M. slevini* was recently described from the 0.8 Km² Gardner islet, east of Floreana Island (Arteaga et al. 2019; Torres-Carvajal 2024). Here, we focus on six allopatric species: *M. albemarlensis* (Isabela Island), *M. bivittatus* (San Cristobal), *M. duncanensis* (Pinzón), *M. grayii* (Floreana), *M. indefatigabilis* (Santa Cruz), and *M. jacobi* (Santiago).

Study site

The Galápagos Archipelago is part of the Galápagos National Park, approximately 1000 Km west of mainland Ecuador, and is formed by 13 main islands and many small islands, islets, and rocks that comprise an area of about 8000 Km² (Snell et al. 1996). Given their volcanic origin, the islands vary in age, with the oldest ones located in the northeast and the youngest in the southwest (Geist et al. 2014). Ocean currents and their equatorial position influence the climate; elevated temperatures and variable rainfall characterize the hot season (January- May), whereas the cool season (June-December) is characterized by constant rainfall and lower temperatures (Trueman and d'Ozouville 2010). The shorelines present rugged coastlines, rocky shores, sandy beaches, mangroves, and lava fields on the younger islands. Further inland, the lower areas are generally dominated by xerophytic trees, shrubs, cacti, and herbs (e.g. *Bursera graveolens*, *Psidium galapagaeum*, *Pisonia floribunda*, *Brachycereus* spp., *Opuntia* spp.) adapted to the arid conditions; as elevation increases and moisture becomes more abundant, these gradually give way to lush forests where ferns and mosses thrive (e.g. *Scalesia* spp., *Miconia robinsoniana*, *Cyathea weatherbyana*) (Jackson 1993; Burdette 2018). Five of the islands of the Archipelago (Baltra, Floreana, Isabela, San Cristobal, Santa Cruz) are inhabited, and the total resident population of the archipelago is 28583 (INEC 2023).

Sampling

From December 2018 to January 2019 and from December 2019 to January 2020, six islands (eight localities) of the Galápagos Archipelago were sampled (Figure 1). Each of these islands is home to endemic species of lava lizards (see Arteaga et al. 2019 for details on their distribution). These localities were chosen based on findings from a previous study that examined the effects of varying degrees of urbanization on the behavior of Galápagos lava lizards, where local populations of lava lizards were identified (Boada-Viteri 2021). At each locality, three non-overlapping linear transects of 4 x 120 m were established, and fecal pellets were collected from leaves, soil, branches, trunks, and leaf litter along linear transects; samples were stored in 96 % ethanol. Sampling at each transect occurred during two time periods: between 8 am and 12 pm and between 1 and 5 pm. A table with the coordinates and elevation of each locality is available in the Supplementary Material (Table S2).

Specimen processing

All fecal samples underwent dissection under a stereomicroscope, and the identifiable organic components were counted and classified to order level (Triplehorn et al. 2005; Gullan and Cranston 2014) to obtain a list of food items. Ant specimens were further sorted into morphospecies. Due to the partial digestion of specimens in the lizard's digestive system, only ant heads were used as reliable indicators for species presence within samples. These heads were point-mounted and identified to subfamily and genus level, using taxonomic keys available at AntWiki (2022) (Fernández and Palacio 2003; Baccaro et al. 2015) and at species-level using keys available in AntWeb (*AntWeb* 2024). We further classified ant species as introduced, non-introduced, or uncertain status following the recent review of the Galápagos ant fauna by Herrera et al. (2024).

Data Analysis

Given that the importance of some food items may have been overestimated due to the local hyperabundance of ants (e.g., when a lava lizard forages near a colony entrance or when an introduced species is ecologically dominant (Krushelnycky et al. 2010), and given the unaccounted variability in food item size, the analyses relied on the number of occurrences (incidence) of each food item across fecal pellets and lava lizard species. Occurrences were

calculated by counting each instance a specific food item appeared within a pellet, regardless of quantity, across all samples and, the following analyses, were made at the family level (Table 2). The dietary breadth of each lava lizard species was quantified using Simpson’s index of diet breadth (MacArthur 1972), represented as:

$$B = \frac{1}{\sum p_i^2}$$

where p_i is the proportion of each food item within the category “i”. A value of B approaching 1 indicates a specialized diet, with higher values suggesting increased diversity in dietary intake. Additionally, the dietary overlap among lava lizard species pairs was calculated using Pianka’s symmetric measure of overlap (Pianka 1973):

$$O_{jk} = \frac{\sum p_{ik} p_{il}}{\sqrt{\sum p_{ik}^2 \sum p_{il}^2}}$$

where O_{jk} is the measure of overlap between species j and k , p_{ik} is the proportion of food item “i” for species “k”, and p_{il} is the same for species “l”. This index ranges from 0, indicating no overlap, to 1, reflecting complete dietary overlap.

We then converted the similarity matrix to a distance matrix using the inverse of Pianka’s similarity measure ($D=1-O$), and a hierarchical cluster analysis was performed. The complete linkage method, which considers the maximum distance between any members of two clusters was used to emphasize the greatest dietary dissimilarities. This approach is well-suited for ecological datasets (Legendre and Legendre 2012). A dendrogram was generated to visually represent the dietary similarities among the species. While all these analyses used the number of occurrences, some results considering the number of specimens for each food item (abundance) across fecal pellets and lava lizard species were also calculated. All analyses were done in R (R Development Core Team 2023).

Additionally, we made casual observations of Galápagos lava lizards in the field sites and took notice of the prey consumed.

Results

In this study, a total of 177 fecal pellets were collected from six species of Galápagos lava lizards (Table 1). Analysis of the samples revealed a total of 7084 food items, categorized into 39 distinct types (Table S3). *M. indefatigabilis* exhibited the highest number of food item categories (n = 32), followed by *M. jacobi* (n = 27), *M. albemarlensis* (n = 23), *M. grayii* (n = 20), *M. bivittatus* (n = 15), and *M. duncanesis* (n = 12).

When considering the total number of food item occurrences across all the fecal pellets found in each *Microlophus* species (n = 941), hymenopterans emerged as the most consumed order, accounting for 73% of the total dietary intake (Table 2). Beetles (Order Coleoptera) were the second most frequent order, making up 15.6% of the diet. The remainder of the diet was composed of a variety of other items, collectively representing 11.4% (Table 2). Overall, ants were the most prevalent food item across all *Microlophus* species, constituting 65% (611 out of 941) of occurrences (Fig. 3). *M. bivittatus* showed the highest relative frequency of ants as a main component of their diet (73.81%) and, *M. jacobi* the lowest (50.37%, Table 2).

A total of 7084 individual food items (i.e., total abundance) were detected. In terms of relative abundance (the total number of food items in each category divided by the total number of food items), Hymenoptera was the most abundant order (n=6565), followed by Coleoptera (307) and plant items (83), with relative frequencies of 92.7%, 4.3%, and 1.2%, respectively. Regarding the latter, it was composed predominantly of small twigs. Additionally, two fecal pellets from *M. jacobi* contained lizard scales and digits. Finally, while not included in the formal analysis, what appeared to be small segments of nylon fishing line were observed in ten fecal pellets (*M. grayii* = 1, *M. indefatigabilis* = 7, and *M. albemarlensis* = 2). Overall, ants were the most abundant food item constituting 90% of all the consumed food items (6375 out of 7084).

A total of 21 species and 6375 ant specimens belonging to 4 subfamilies were identified from the fecal pellets (Fig. 2, Table 3). Of these, 13 were introduced species, constituting, in terms of occurrences, 87.9% of the ant records (537 out of 611) and 88.2% (5623 out of 6375) of the abundance of ants. Overall, introduced ant species accounted for 57.1% of the occurrences (537 out of 941) and 79.4% (5623 out of 7084) of the total food item abundance.

The Simpson's Index of Breadth of Diet values found (*M. albemarlensis* = 1.96, *M. bivittatus* = 1.79, *M. duncanensis* = 2.31, *M. grayii* = 2.45, *M. indefatigabilis* = 2.08, *M. jacobi* = 3.44) suggest that the Galápagos lava lizard species studied have a narrow diet. Based on the total number of occurrences we calculated the relative proportion of each food item, a chi-square goodness-of-fit test that confirmed ants are consumed in significantly higher proportion (64.9%) than other items ($X^2_{(18)} = 7025.1$, $p < 0.001$) and are a dominant component of their diet (Fig. 3).

Regarding Pianka's symmetric measure of overlap, a mean value of 0.70 was found, indicating a mean relatively high overlap. The least dietary overlap occurs between *M. duncanensis* and *M. bivittatus* (0.39), and the greatest between *M. indefatigabilis* and *M. albemarlensis* (0.89) (Fig. 4). A hierarchical clustering dendrogram (Fig. 5), based on the inverse Pianka's overlap index, identified *M. bivittatus* as having the most distinct dietary preferences. Additionally, two other clusters emerged: one consisting of *M. grayii* with *M. albemarlensis* and *M. indefatigabilis*, and another grouping *M. duncanensis* with *M. jacobi*.

During fieldwork observed numerous instances where Galápagos lava lizards were actively hunting large prey. We captured photographs of them feeding on introduced paper wasps, *Polistes versicolor*; an introduced house gecko, *Hemidactylus frenatus*; an unidentified earthworm; an endemic grasshopper, *Schistocerca melanocera*; and a spider exuviae (Fig. 6). Additionally, although not photographed, we observed two instances of a female *M. albemarlensis* preying on a centipede, *Scolopendra galapagoensis*, and a male on an unidentified gecko.

Discussion

In this study, we obtained fecal pellet samples from six endemic Galápagos lava lizard species and sorted and identified the food items present. We confirmed that both in terms of the number of occurrences and abundance, ants were the most highly prevalent food item. Moreover, we found that within ants, over 80% of the occurrences and 88% of the abundance were made of introduced species. The presence of ants in the diet of lava lizards in the continent has been a common encounter before. For instance, regarding the number of items consumed, Pérez Z et al. (2015) found that ants were the most consumed item (44.1%) in the diet of the Peruvian desert

coastal lizard *M. thoracicus*. In general, *Microlophus* spp. exhibit diverse dietary habits, with invertebrates and native ants comprising an important proportion of the diet of some species (Denburgh and Slevin 1913; Chávez-Villavicencio et al. 2018; Toyama et al. 2018; Beuttner and Koch 2019) (Fig. 6).

This study provides the first documentation of a high prevalence of ants, mainly introduced, in the diet of Galápagos lava lizards. Since the early stomach content analyses of Galápagos lava lizards by Denburgh and Slevin (1913), no comprehensive diet composition studies have been conducted. For *M. duncanensis*, for instance, they mention: “*Their food consists exclusively of insects. The stomachs examined contained grasshoppers, caterpillars, grubs, beetles, etc.*” Similarly, for *M. delanonis* (not included in this study): “*(...) the food (...) consists of grasshoppers, beetles, caterpillars, seed-capsules and berries*”. About *M. albemarlensis* they say: “*All stomachs examined contained insects, chiefly Orthoptera*” and, “*Stomachs (...) contained insects and spiders; (...) insects (...) spiders, insects and seeds (...) farther inland insects (...) are eaten*”. Notably, these accounts do not mention ants, despite many of the same introduced species we identified being already present during that time (e.g. *S. geminata*, *T. melanocephalum*, *O. bauri* (Emery, C. 1893); *S. globularia* (Wheeler 1919), *W. auropunctatta*, (Silberglie, R. 1972)), and the presence of native species. More recently, however, Lewbart et al. (2017) identified ants as the predominant food item by number for *M. indefatigabilis*. Coupled with our findings, this may indicate a dietary shift associated with the increased prevalence of introduced ants.

The increase in the introduction of exotic ant species during the mid and late-20th century (Herrera et al. 2020; Herrera et al. 2024) might have fueled such a dietary shift towards a high proportion of introduced ants, as a response to altered food availability. In the Galápagos, while there are some species whose status is not clear, non-native ant species vastly outnumber native taxa in the order of 3:1 (Herrera et al. 2020; Herrera et al. 2024). Following that pattern, 13 out of the 21 ant species we identified corresponded to introduced species. Some of these are known to displace native invertebrates and achieve high population densities (e.g. *P. longicornis* (Wetterer 2008); *S. geminata* (Wetterer 2011), *W. auropunctatta* (Clark et al. 1982)), thus becoming the most readily available prey for lava lizards while simultaneously hindering the

availability of other prey. The high predominance of introduced ants in the diet of Galápagos lava lizards could negatively impact their nutritional intake and overall health, considering the possible differences in nutritional value between native invertebrate species and introduced ants (Suarez and Case 2002), reduced palatability or even toxic nature of introduced ants (Suarez et al. 2000; Venable and Langkilde 2022), lower capture success or lower net energetic gain given the need to consume more prey to compensate for the larger prey that introduced ants displace (Suarez and Case 2002) disruption of foraging (Langkilde 2009; Venable and Langkilde 2022), and fleeing behaviors (Trompeter and Langkilde 2011). Furthermore, many Galápagos lava lizard species forage and seek refuge in microhabitats similar to those used by introduced ants for nesting and foraging (Blüthgen and Feldhaar 2010) (e.g. around shrubs and bushes, under rocks and logs, in leaf litter and rock crevices, (Denburgh and Slevin 1913), thereby increasing the likelihood of direct interactions between the lizards and alien ant species.

In addition to the direct effects, invasive ants are generally expected to lower native species diversity through indirect effects arising from the local extinction of certain species (Tercel et al. 2023), which might ultimately impact lava lizard populations. As observed for Horned lizards (Suarez et al. 2000; Allen et al. 2004), an abundance of introduced ants might result in a decline of native insect species, both in terms of diversity and abundance (Rowles and O'Dowd 2009), upon which Galápagos lava lizards rely. Furthermore, the documented ecological services provided by Galápagos lava lizards (e.g. pest control, as food, pollination, seed dispersal) could be diminished or interrupted, potentially leading to the extinction of the native plant and animal species dependent on them (Holway et al. 2002; Traveset and Richardson 2006; Lach and Hooper-Bùi 2010). Ultimately, as observed in other lizard species, the presence of aggressive introduced ants, such as fire ants, can lead to a reduction in recruitment and population size in invaded areas (e.g. fence lizards (Darracq et al. 2017), horned lizards (Donaldson, W. et al. 1994), skinks (Feare, C. 1999; Lach et al. 2022)). Although no Galápagos lava lizard species are currently considered endangered (CITES 2024; IUCN 2024), the study of the effects of ant introductions on the archipelago remains crucial, considering the dynamic nature of these ecological interactions and escalating anthropogenic pressures.

Regarding the ant species ingested by Galápagos lava lizards, noteworthy findings include the consumption of *Brachymyrmex* by *M. jacobii*, despite no previous records of this genus on Santiago Island. Although identification was hindered by the fact that we only found head capsules, these specimens are likely *B. heeri*, present in natural and disturbed habitats on neighboring islands and considered a minor threat (Herrera et al. 2020). This suggests a potential range expansion of this introduced species, warranting further investigation. Interestingly, some highly invasive ant species were not detected. For example, *Pheidole megacephala*, one of the most destructive invasive species worldwide (Lowe et al. 2000; Wetterer 2007), and reported in Isabela, Santa Cruz, and San Cristobal Islands (Herrera et al. 2013; Herrera et al. 2020), was absent in our samples. This species has been detected on many oceanic islands (Wetterer 2007) and recently, on Ecuador's mainland (Salazar-Basurto et al. 2023). Its absence could be attributed to the conservation integrity of our sampling sites and their remoteness, as it prefers disturbed habitats (Wetterer 2007; Herrera et al. 2020). Alternatively, Galápagos lava lizards might avoid this species due to its aggressiveness, similar to observations in other lizard species (e.g., Suarez et al. 2000; Ramakrishnan et al. 2018), potentially explaining the absence of other invasive species such as *Cardiocondyla minutior*, *Monomorium pharaonis*, *Tetramorium bicarinatum*, *Trychomyrmex destructor*, and *Odontomachus ruginodis* (Herrera et al. 2020). Further sampling at the study sites, incorporating active and passive techniques (Nicholas J. Gotelli et al. 2011), could provide insights into the specific ant species present, and facilitate monitoring for new alien species introductions.

Besides these, there were also notable deviations in the diet of some lava lizards from their typical consumption of small arthropods and plant material. For the first time, vertebrate remains have been identified in the diet of the Santiago lava lizard, *M. jacobii*, specifically scales and digits from a conspecific, based on the lack of correspondence with Gekkonidae lizards, the only other similar-sized saurians on the Island, we are almost certain that these correspond to a conspecific. The consumption of vertebrates, including finch hatchlings, geckos, and conspecifics (particularly juveniles), has been documented at low frequencies in six of the ten Galápagos lava lizard species (*M. barringtonensis*, *M. delanonis*, *M. habelii*, *M. indefatigabilis*, *M. jacobii*, and *M. pacificus* (Lewbart et al. 2017; Moore et al. 2017; Arteaga et al. 2019; Crespo-Pérez 2023)), as this would be an ancestral behavior within the genus (Labra et al. 2022).

However, this observation grants further investigation to confirm the identity of the consumed saurians as either conspecifics or as gekkonid lizards. Additionally, our finding of fishing line fragments in species from three populated islands warrants further investigation, considering that Galápagos lava lizards inhabit areas close to beaches and coastal ecosystems (Benavides et al. 2009; Boada-Viteri 2021) where they may encounter this type of human-derived solid contaminants. While the impacts of ingesting plastics on reptiles remain poorly understood (Hou and Rao 2022), we recommend further investigation, especially on human-inhabited islands where exposure may be more prevalent.

In addition to findings from the fecal pellet analysis, which predominantly consisted of small-sized prey, field site observations revealed the ingestion of larger prey by Galápagos lava lizards. These instances included predation on other saurians, as previously documented elsewhere. Furthermore, we observed these lizards actively hunting large and fast (e.g., grasshoppers, *S. melanocera*), flying and venomous (*P. versicolor*) and fast, venomous prey such as centipedes (*S. galapagoensis*). Previously, there have been observations of Galápagos lava lizards feeding on large prey such as newly-hatched finches, centipedes, moths, spiders and dragonflies (Moore et al. 2017). These observations characterize Galápagos lava lizards as ground-dwelling diurnal lizards (Stebbins et al. 1967; Rowe, J.W. et al. 2019) that spend most of their time basking in the sun relying on a “sit-and-wait” strategy (Boada-Viteri 2021). This behavior likely contributes to the high prevalence of primarily ant foragers, especially invasive ant species that may reach high densities (Lach and Hooper-Bùi 2010), in their diet. Nevertheless, they are also highly skilled hunters capturing sizeable prey (e.g., finch hatchlings, other saurians), as well as rapidly moving (e.g., grasshoppers) or flying prey (e.g., moths, paper wasps), including some capable of injecting venom (e.g., centipedes, paper wasps). This versatility in hunting strategy underscores their adaptability and highlights the dynamic nature of their dietary habits which can also include non-native species.

In terms of the diet composition among the Galápagos lava lizards, *M. indefatigabilis* (Santa Cruz Island) and *M. albemarlensis* (Isabela) shared the most food items, whereas *M. duncanensis* (Pinzón) and *M. bivittatus* (San Cristobal) shared the fewest. This variation could be partially attributed to the geographical distance between the islands (approximately 28 km between

Isabela and Santa Cruz compared to 120 km between Pinzón and San Cristobal), which might influence the exchange of species between islands. Furthermore, our dendrogram indicates that *M. bivittatus* exhibits the least similarity with the other species studied. This aligns with the hypothesis that Galápagos lava lizard species on the southeastern, older islands derive from older lineages than those on the northwestern islands (Benavides et al. 2009). *M. bivittatus* is also the only species in our study from the so-called “Eastern radiation” and the ‘oldest’ in our study. For the remaining species, it is unclear whether the evolutionary history of island colonization influences diet, but notably, these species belong to the “Western radiation” clade (Benavides et al., 2009). Given the scope of our study, pinpointing the primary factors driving the diet composition of Galápagos lava lizards remains challenging. Nonetheless, beyond their evolutionary history, the increased movement of people and goods among the islands and from the mainland (Quiroga, D. 2018; Stahl, P.W. et al. 2020; Sampedro et al. 2020) likely plays a significant role, as non-native species find more ways to expand their range.

The high prevalence of ants in Galápagos lava lizards’ diets is clear, yet certain limitations of our methodology warrant consideration. Firstly, samples had already passed through the lizards’ digestive systems, and ants had to be identified based mostly on cephalic capsules. This limited our ability to identify rarer species, as crucial morphological details on the body and legs were often absent. Moreover, it likely led to an underrepresentation of soft food items like larvae, worms, and soft plant material, which may not survive digestion or could decompose before sample collection (Pincheira-Donoso 2008; Pérez-Mellado et al. 2011). A testament to the latter is that we attempted to barcode ant morphospecies for species confirmation (Smith and Fisher 2009), but were unsuccessful. Using fecal pellets also precluded the identification of the lizards’ sex and life stages, as well as the assessment of the volume and nutritional value of the food items. Finally, our sampling was restricted to the transition period between the dry and wet seasons (Trueman and d’Ozouville 2010); more research throughout the year is necessary to fully understand seasonal dietary variations. Despite these limitations, fecal pellets analysis offers an affordable and non-invasive means to study the diet of Galápagos lava lizards and could be used to monitor the introduction of alien species, as evidenced by our discovery of *Brachymyrmex* on Santiago.

In summary, our study sheds light on the understanding of the ecological dynamics affecting Galápagos lava lizards, amidst an ongoing invasion process. The high prevalence of introduced ant species in the diets of these lizards' points to a shift in their dietary habits, possibly driven by their high availability and the diminished abundance of other prey. This may have profound implications for the nutritional health, behavior, and survival of lava lizards, thereby affecting the ecological services they provide and the broader ecosystem balance. Our findings underscore the critical need for continuous monitoring and research to elucidate the long-term impacts of these dietary changes and to develop effective conservation strategies. By fostering a deeper understanding of these complex ecological interactions, we can better safeguard the Galápagos Islands' biodiversity against the challenges posed by biological invasions.

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References

- Allen CR, Epperson DM, Garmestani AS (2004) Red Imported Fire Ant Impacts on Wildlife: A Decade of Research. *amid* 152(1):88–103. [https://doi.org/10.1674/0003-0031\(2004\)152\[0088:RIFAIO\]2.0.CO;2](https://doi.org/10.1674/0003-0031(2004)152[0088:RIFAIO]2.0.CO;2)
- AntWiki (2022) Key to Subfamilies of the Neotropical Region. In: AntWiki: The Ants - Online. https://www.antwiki.org/wiki/Key_to_subfamilies_of_the_Neotropical_region#cite_note-1. Accessed 2 Jun 2023
- Arnan X, Andersen AN, Gibb H, Parr CL, Sanders NJ, Dunn RR, Angulo E, Baccaro FB, Bishop TR, Boulay R, Castracani C, Cerdá X, Toro ID, Delsinne T, Donoso DA, Elten EK, Fayle TM, Fitzpatrick MC, Gómez C, Grasso DA, Grossman BF, Guénard B, Gunawardene N, Heterick B, Hoffmann BD, Janda M, Jenkins CN, Klimes P, Lach L, Laeger T, Leponce

- M, Lucky A, Majer J, Menke S, Mezger D, Mori A, Moses J, Munyai TC, Paknia O, Pfeiffer M, Philpott SM, Souza JLP, Tista M, Vasconcelos HL, Retana J (2018) Dominance–diversity relationships in ant communities differ with invasion. *Global Change Biology* 24(10):4614–4625. <https://doi.org/10.1111/gcb.14331>
- Arteaga A, Bustamante L, Vieira J, Tapia J, Guayasamín J (2019) Reptiles of the Galapagos: life on the Enchanted Islands. Tropical Herping, Quito, Ecuador
- Baccaro FB, Feitosa RM, Fernández F, Fernandes IO, Izzo TJ, Souza JD, Solar R (2015) Guia para os gêneros de formigas do Brasil. Editora INPA
- Benavides E, Baum R, McClellan D, Sites JW (2007) Molecular Phylogenetics of the Lizard Genus *Microlophus* (Squamata:Tropiduridae): Aligning and Retrieving Indel Signal from Nuclear Introns. *Systematic Biology* 56(5):776–797. <https://doi.org/10.1080/10635150701618527>
- Benavides E, Baum R, Snell HM, Snell HL, Sites Jr Jack W (2009) Island Biogeography of Galapagos Lava Lizards (Tropiduridae: *Microlophus*): Species Diversity and Colonization of the Archipelago. *Evolution* 63(6):1606–1626. <https://doi.org/10.1111/j.1558-5646.2009.00617.x>
- Bertelsmeier C, Ollier S, Liebhold A, Keller L (2017) Recent human history governs global ant invasion dynamics. *Nat Ecol Evol* 1(7):1–8. <https://doi.org/10.1038/s41559-017-0184>
- Beuttner A, Koch C (2019) Analysis of diet composition and morphological characters of the Peruvian lizard *Microlophus stolzmanni* (Squamata: Tropiduridae). *Phyllomedusa* 18:47–62. <https://doi.org/10.11606/issn.2316-9079.v18i1p47-62>
- Blüthgen N, Feldhaar H (2010) Food and Shelter: How Resources Influence Ant Ecology. In: Lach L, Parr CL, Abbott KL (eds) *Ant Ecology*. Oxford University Press, New York, pp 115–136
- Boada-Viteri E (2021) Behavioural Partitioning of Mainland and Island Lava Lizard Assemblages in Ecuador. Doctoral Thesis, La Trobe
- Burdette C (2018) Galápagos Islands, off the coast of Ecuador. In: World Wildlife Fund. <https://www.worldwildlife.org/ecoregions/nt1307>. Accessed 26 Oct 2023
- Burger J, Gochfeld M (1993) Tourism and Short-term Behavioural Responses of Nesting Masked, Red-footed, and Blue-footed, Boobies in the Galápagos. *Environmental Conservation* 20(3):255–259. <https://doi.org/10.1017/S0376892900023043>
- Causton CE, Peck SB, Sinclair BJ, Roque-Albelo L, Hodgson CJ, Landry B (2006) Alien Insects: Threats and Implications for Conservation of Galápagos Islands. *Annals of the Entomological Society of America* 99(1):121–143. [https://doi.org/10.1603/0013-8746\(2006\)099\[0121:AITAIF\]2.0.CO;2](https://doi.org/10.1603/0013-8746(2006)099[0121:AITAIF]2.0.CO;2)

- Chávez-Villavicencio C, Ibáñez-Álvarez Y, Charcape-Ravelo JM (2018) Selección de hábitat y composición de la dieta de *Microlophus occipitalis* (Reptilia: Tropicuridae) en Sechura, Piura - Perú. *Revista Peruana de Biología* 25(3):221–228. <https://doi.org/10.15381/rpb.v25i3.13403>
- CITES (2024) Convention on International Trade in Endangered Species of Wild Fauna and Flora. www.cites.org. Accessed 29 Feb 2024
- Clark DB, Guayasamin C, Pazmino O, Donoso C, de Villacis YP (1982) The Tramp Ant *Wasmannia auropunctata*: Autecology and Effects on Ant Diversity and Distribution on Santa Cruz Island, Galapagos. *Biotropica* 14(3):196–207. <https://doi.org/10.2307/2388026>
- Crespo-Pérez V (2023) Cannibalism in a Santa Cruz Lava Lizard *Microlophus indefatigabilis* (Tropicuridae), in the Galapagos Islands. *Revista Latinoamericana de Herpetología* 6(4):e815 (78-80). <https://doi.org/10.22201/fc.25942158e.2023.4.815>
- Darracq AK, Smith LL, Oi DH, Conner LM, McCleery RA (2017) Invasive ants influence native lizard populations. *Ecosphere* 8(1):e01657. <https://doi.org/10.1002/ecs2.1657>
- Denburgh JV, Slevin JR (1913) Van Denburgh, J. and Slevin, J. R. 1913. Expedition of the California Academy of Sciences to the Galápagos Islands, 1905-1906. The Galapagoan lizards of the genus *Tropicurus*; with notes on the iguanas of the genera *Conolophus* and *Amblyrhynchus*. *Proceedings of the California Academy of Sciences* 2:133–202
- Donaldson, W., Price, A.H., Morse, J. (1994) The current status and future prospects of the Texas horned lizard (*Phrynosoma cornutum*) in Texas. *Texas Journal of Science* 46(2):97–113
- Emery, C. (1893) Notice sur quelques fourmis des îles Galapagos. *Annales de la Société Entomologique de France* 62:89–92
- Feare, C. (1999) Ants take over from rats on Bird Island, Seychelles. *Bird Conservation International* 9(1):95–96
- Fernández F, Palacio EE (2003) Clave para las subfamilias y géneros. In: Fernández F (ed) *Introducción a las Hormigas de la Región Neotropical*. Instituto de Investigación de Recursos Biológicos Alexander von Humboldt, Bogotá, Colombia, pp 233–260
- French SS, DeNardo DF, Greives TJ, Strand CR, Demas GE (2010) Human disturbance alters endocrine and immune responses in the Galapagos marine iguana (*Amblyrhynchus cristatus*). *Hormones and Behavior* 58(5):792–799. <https://doi.org/10.1016/j.yhbeh.2010.08.001>
- Gan JYS, Pathy TS, Yeo DYC, Lee JM, Yek SH (2022) The population dynamics of the yellow crazy ant *Anoplolepis gracilipes* (Hymenoptera: Formicidae) on a tropical island in Malaysia. *Ecological Entomology* 47(3):339–346. <https://doi.org/10.1111/een.13119>

- Geist DJ, Snell H, Snell H, Goddard C, Kurz MD (2014) A Paleogeographic Model of the Galápagos Islands and Biogeographical and Evolutionary Implications. In: The Galápagos. American Geophysical Union (AGU), pp 145–166
- Gullan PJ, Cranston PS (2014) *The Insects: An Outline of Entomology*. John Wiley & Sons
- Hernández-Teixidor D, Pérez-Delgado AJ, Suárez D, Reyes-López J (2020) Six new non-native ants (Formicidae) in the Canary Islands and their possible impacts. *Journal of Applied Entomology* 144(6):434–441. <https://doi.org/10.1111/jen.12751>
- Herrera HW (2014) CDF Checklist of Galápagos Ants - FCD Lista de Especies de Hormigas de Galápagos. In: Bungartz F, Herrera H, Jaramillo P, Tirado N, Jiménez-Uzcátegui G, Ruiz D, Guézou A, Ziemmeck F (eds) *Charles Darwin Foundation Galápagos Species Checklist - Lista de Especies de Galápagos de la Fundación Charles Darwin*. Charles Darwin Foundation / Fundación Charles Darwin, Puerto Ayora, Galápagos
- Herrera HW, Baert L, Dekoninck W, Causton CE, Sevilla CR, Pozo P, Hendrickx F (2020) Distribution and habitat preferences of Galápagos ants (Hymenoptera: Formicidae)
- Herrera HW, Sevilla CR, Dekoninck W (2013) *Pheidole megacephala* (Fabricius 1793) (Hymenoptera: Formicidae): a new invasive ant in the Galápagos Islands. *panp* 89(4):234–243. <https://doi.org/10.3956/2013-16.1>
- Herrera HW, Tocora MC, Fiorentino G, Causton CE, Dekoninck W, Hendrickx F (2024) The ants of the Galápagos Islands (Hymenoptera, Formicidae): a historical overview, checklist, and identification key. *Zookeys* 1191:151–213. <https://doi.org/10.3897/zookeys.1191.107324>
- Hervías-Parejo S, Heleno R, Rumeu B, Guzmán B, Vargas P, Olesen JM, Traveset A, Vera C, Benavides E, Nogales M (2019) Small size does not restrain frugivory and seed dispersal across the evolutionary radiation of Galápagos lava lizards. *Current Zoology* 65(4):353–361. <https://doi.org/10.1093/cz/zoy066>
- Hervías-Parejo S, Nogales M, Guzmán B, Trigo M del M, Olesen JM, Vargas P, Heleno R, Traveset A (2020) Potential role of lava lizards as pollinators across the Galápagos Islands. *Integrative Zoology* 15(2):144–148. <https://doi.org/10.1111/1749-4877.12386>
- Hoffmann BD, Ducarme F, Bradford D, Martinez S (2023) Spread of stinging ants to oceanic islands, and the need to raise awareness of prevention and treatment of ant stings. *Emergency Medicine Australasia* 35(4):560–563. <https://doi.org/10.1111/1742-6723.14165>
- Holway DA, Lach L, Suarez AV, Tsutsui ND, Case TJ (2002) The causes and consequences of ant invasions. *Annu Rev Ecol Syst* 33:181–233
- Hou D-M, Rao D-Q (2022) Microplastics: Their Effects on Amphibians and Reptiles-A Review. *PJZ* 54(6). <https://doi.org/10.17582/journal.pjz/20210820080823>

- INEC (2023) Data y Resultados. In: Instituto Nacional de Estadística y Censos de Ecuador. <https://www.censoecuador.gob.ec/data-y-resultados/>. Accessed 26 Oct 2023
- IUCN (2024) The IUCN Red List of Threatened Species. Version 2023-1. www.iucnredlist.org/. Accessed 29 Feb 2024
- Jackson MH (1993) Galapagos: A Natural History. University of Calgary Press, Canada
- Jourdan H, Sadler R, Bauer A (2001) Little fire ant invasion (*Wasmannia auropunctata*) as a threat to New Caledonian lizards: evidences from a sclerophyll forest (Hymenoptera: Formicidae). *Sociobiology* 38(3):283–302
- Krushelnycky PD, Holway DA, LeBrun EG (2010) Invasion Processes and Causes of Success. In: Lach L, Parr CL, Abbott KL (eds) *Ant Ecology*. Oxford University Press, pp 245–260
- Labra A, Daigre M, Imil V (2022) Cannibalism in *Microlophus* Lizards. *Journal of Herpetology* 56(1):67–74. <https://doi.org/10.1670/20-132>
- Lach L, Case D, Yeeles P, Hoskin CJ (2022) Invasive ants reduce abundance of small rainforest skinks. *Biodivers Conserv* 31(3):739–755. <https://doi.org/10.1007/s10531-022-02360-6>
- Lach L, Hooper-Bùi LM (2010) Consequences of ant invasions. In: Lach L, Parr CL, Abbott KL (eds) *Ant Ecology*. Oxford University Press, Oxford, pp 261–286
- Langkilde T (2009) Invasive fire ants alter behavior and morphology of native lizards. *Ecology* 90(1):208–217
- Legendre P, Legendre L (2012) *Numerical Ecology*, Third Edition. Elsevier
- Lewbart GA, Valle C, Muñoz-Pérez JP (2017) *Microlophus indefatigabilis*. *Herpetological Review* 48(4):852
- Lowe S, Browne M, Boudjelas S, De Poorter M (2004) 100 of the World's Worst Invasive Alien Species: A Selection from the Global Invasive Species Database. The Invasive Species Specialist Group (ISSG) a specialist group of the Species Survival Commission (SSC) of the World Conservation Union (IUCN)
- Lowe S, Browne M, Boudlejas S (2000) 100 of the world's worst invasive alien species. *Aliens* 12:1–12
- Lubin Y (1985) Studies of the Little Fire Ant, *Wasmannia auropunctata* in a Niño year. In: Robinson G, Del Pino E (eds) *El Niño en las Islas Galápagos: el Evento de 1982–1983*. Charles Darwin Foundation, Quito, pp 473–493
- MacArthur RH (1972) *Geographical Ecology: Patterns in the Distribution of Species*. Harper & Row New York

- Medrano-Vizcaíno P, Brito-Zapata D, Rueda-Vera A, Jarrín-V P, García-Carrasco J-M, Medina D, Aguilar J, Acosta-Buenaño N, González-Suárez M (2023) First national assessment of wildlife mortality in Ecuador: An effort from citizens and academia to collect roadkill data at country scale. *Ecology and Evolution* 13(3):e9916. <https://doi.org/10.1002/ece3.9916>
- Moore TY, Cooper KL, Biewener AA, Vasudevan R (2017) Unpredictability of escape trajectory explains predator evasion ability and microhabitat preference of desert rodents. *Nature Communications* 2017 8:1 8(1):1–9. <https://doi.org/10.1038/s41467-017-00373-2>
- Naughton I, Boser C, Tsutsui ND, Holway DA (2020) Direct evidence of native ant displacement by the Argentine ant in island ecosystems. *Biol Invasions* 22(2):681–691. <https://doi.org/10.1007/s10530-019-02121-7>
- Nicholas J. Gotelli, Aaron M. Ellison, Robert R. Dunn, Nathan J. Sanders (2011) Counting ants (Hymenoptera: Formicidae): biodiversity sampling and statistical analysis for myrmecologists. *Myrmecological News* 15:13–19. https://doi.org/10.25849/MYRMECOL.NEWS_015:013
- Pérez Z J, Fuentes E, Jordán J (2015) Dieta de la lagartija de los gramadales *Microlophus thoracicus icae* en el valle del río Ica, Perú. *Revista Peruana de Biología* 22(2):233–238
- Pérez-Mellado V, Pérez-Cembranos A, Garrido M, Luiselli L, Corti C (2011) Using faecal samples in lizard dietary studies. *Amphibia-Reptilia* 32(1):1–7. <https://doi.org/10.1163/017353710X530212>
- Pianka E (1973) The structure of lizard communities. *Annual Review of Ecology and Systematics* 4:53–74
- Pincheira-Donoso D (2008) Testing the Accuracy of Fecal-Based Analyses in Studies of Trophic Ecology in Lizards. *Copeia* 2008(2):322–325. <https://doi.org/10.1643/CE-06-214>
- Quiroga, D. (2018) Understanding Invasive Species in the Galapagos Islands: From the Molecular to the Landscape. In: Torres, M.L., Mena, C.F. (eds) *Understanding Invasive Species in the Galapagos Islands: From the Molecular to the Landscape*. Springer, Cham, Switzerland
- R Development Core Team, Team RDC (2023) R: A Language and Environment for Statistical Computing. *R Foundation for Statistical Computing* 1:409
- Ramakrishnan S, Wolf AJ, Hellgren EC, Moody RW, Bogosian V III (2018) Diet Selection by a Lizard Ant-Specialist in an Urban System Bereft of Preferred Prey. *Journal of Herpetology* 52(1):79–85. <https://doi.org/10.1670/16-072>
- Rowe, J.W., Martin, C.E., Clark, D.L., Valle, C., Vintimilla-Palacios, C.P. (2019) Habitat Use and Spatial Ecology of Three *Microlophus* Lizard Species from Santa Cruz and San Cristóbal Islands, Galápagos, and the Coastal Dry Forest of Machalilla, Ecuador. *Herpetological Review* 50(1):43–51

- Rowles AD, O'Dowd DJ (2009) New mutualism for old: indirect disruption and direct facilitation of seed dispersal following Argentine ant invasion. *Oecologia* 158(4):709–716. <https://doi.org/10.1007/s00442-008-1171-2>
- Salazar-Basurto J, Troya A, Romero, F., Wild AL, Pazmiño-Palomino A (2023) They arrived and don't stop coming: an update on the distribution of exotic ants (Hymenoptera, Formicidae) in continental Ecuador. *Check List* 19(6). <https://doi.org/10.15560/19.6.801>
- Sampedro C, Pizzitutti F, Quiroga D, Walsh SJ, Mena CF (2020) Food supply system dynamics in the Galapagos Islands: agriculture, livestock and imports. *Renewable Agriculture and Food Systems* 35(3):234–248. <https://doi.org/10.1017/S1742170518000534>
- Silberglied, R. (1972) The little fire ant, *Wasmannia auropunctata*, a serious pest in the Galapagos island. *Noticias de Galápagos* 19:13–15
- Smith MA, Fisher BL (2009) Invasions, DNA barcodes, and rapid biodiversity assessment using ants of Mauritius. *Frontiers in Zoology* 6:31–31. <https://doi.org/10.1186/1742-9994-6-31>
- Snell HL, Jennings RD, Snell HM, Harcourt S (1988) Intrapopulation variation in predator-avoidance performance of Galápagos lava lizards: The interaction of sexual and natural selection. *Evol Ecol* 2(4):353–369. <https://doi.org/10.1007/BF02207566>
- Snell HM, Stone PA, Snell HL (1996) A summary of geographical characteristics of the Galapagos Islands. *Journal of Biogeography* 23(5):619–624. <https://doi.org/10.1111/j.1365-2699.1996.tb00022.x>
- Stahl, P.W., Astudillo, F.J., Jamieson, R.W., Quiroga, D., Delgado, F. (2020) *Historical Ecology and Archaeology in the Galápagos Islands: A Legacy of Human Occupation*. University Press of Florida, Gainesville, FL
- Stebbins RC, Lowenstein JM, Cohen NW (1967) A Field Study of the Lava Lizard (*Tropidurus albemarlensis*) in the Galapagos Islands. *Ecology* 48(5):839–851. <https://doi.org/10.2307/1933742>
- Suarez AV, Case TJ (2002) Bottom-up Effects on Persistence of a Specialist Predator: Ant Invasions and Horned Lizards. *Ecological Applications* 12(1):291–298. [https://doi.org/10.1890/1051-0761\(2002\)012\[0291:BUEOPO\]2.0.CO;2](https://doi.org/10.1890/1051-0761(2002)012[0291:BUEOPO]2.0.CO;2)
- Suarez AV, Richmond JQ, Case TJ (2000) Prey Selection in Horned Lizards Following the Invasion of Argentine Ants in Southern California. *Ecological Applications* 10(3):711–725. [https://doi.org/10.1890/1051-0761\(2000\)010\[0711:PSIHLF\]2.0.CO;2](https://doi.org/10.1890/1051-0761(2000)010[0711:PSIHLF]2.0.CO;2)
- Tanner D, Perry J (2007) Road effects on abundance and fitness of Galápagos lava lizards (*Microlophus albemarlensis*). *Journal of Environmental Management* 85(2):270–278. <https://doi.org/10.1016/j.jenvman.2006.08.022>

- Terrel MPTG, Cuff JP, Symondson WOC, Vaughan IP (2023) Non-native ants drive dramatic declines in animal community diversity: A meta-analysis. *Insect Conservation and Diversity* 16(6):733–744. <https://doi.org/10.1111/icad.12672>
- Toral-Granda MV, Causton CE, Jäger H, Trueman M, Izurieta JC, Araujo E, Cruz M, Zander KK, Izurieta A, Garnett ST (2017) Alien species pathways to the Galapagos Islands, Ecuador. *PLOS ONE* 12(9):e0184379. <https://doi.org/10.1371/journal.pone.0184379>
- Torres-Carvajal O (2024) A new species of lava lizard (Iguanidae: Tropidurinae: *Microlophus*) from the Galápagos. *Zootaxa* 5428(1):58–74. <https://doi.org/10.11646/zootaxa.5428.1.2>
- Toyama KS, Junes K, Ruiz J, Mendoza A, Pérez JM (2018) Ontogenetic Changes in the Diet and Head Morphology of an Omnivorous Tropidurid Lizard (*Microlophus thoracicus*). *Zoology* 129:45–53. <https://doi.org/10.1016/j.zool.2018.06.004>
- Traveset A, Richardson DM (2006) Biological invasions as disruptors of plant reproductive mutualisms. *Trends in Ecology & Evolution* 21(4):208–216. <https://doi.org/10.1016/j.tree.2006.01.006>
- Triplehorn CA, Johnson NF, Borror DJ (2005) Borror and Delong’s Introduction to the Study of Insects, 7th Ed. Thomson, Australia
- Trompeter WP, Langkilde T (2011) Invader danger: Lizards faced with novel predators exhibit an altered behavioral response to stress. *Hormones and Behavior* 60(2):152–158. <https://doi.org/10.1016/j.yhbeh.2011.04.001>
- Trueman M, d’Ozouville N (2010) Characterizing the Galapagos terrestrial climate in the face of global climate change. *Galapagos Research* 67:26–37
- Ujiyama S, Tsuji K (2018) Controlling invasive ant species: a theoretical strategy for efficient monitoring in the early stage of invasion. *Sci Rep* 8(1):8033. <https://doi.org/10.1038/s41598-018-26406-4>
- Venable CP, Langkilde T (2022) Avoidance of invasive prey reduces subsequent consumption of similar native prey. *Food Webs* 32:e00247. <https://doi.org/10.1016/j.fooweb.2022.e00247>
- Wauters N, Dekoninck W, Nagy Z, Fournier D (2018) Impact of laying date and fire ants on hatchlings of *Chelonoidis porteri* on Santa Cruz Island, Galápagos, Ecuador. *Herpetological Conservation and Biology* 13(2):479–487
- Webb SL, Henke SE (2003) Defensive Strategies of Texas Horned Lizards (*Phrynosoma cornutum*) Against Red Imported Fire Ants. *Herpetological Review* 34(4):327–328
- Wetterer JK (2008) Worldwide spread of the longhorn crazy ant, *Paratrechina longicornis* (Hymenoptera: Formicidae). *Myrmecological News* 11:137–149
- Wetterer JK (2011) Worldwide spread of the tropical fire ant, *Solenopsis geminata* (Hymenoptera: Formicidae). *Myrmecological News* 14:21–35

Wetterer JK (2007) Biology and impacts of Pacific Island invasive species. 3. The African big-headed ant, *Pheidole megacephala* (Hymenoptera: Formicidae). *Pacific Science* 61(4):437–456

Wheeler WM (1919) Expedition of the California Academy of Sciences to the Galapagos Islands, 1905-1906. XV. The ants of Cocos Island. *Proceedings of the California Academy of Sciences* 4(2):299–308

Zylberberg M, Lee KA, Klasing KC, Wikelski M (2013) Variation with Land Use of Immune Function and Prevalence of Avian Pox in Galapagos Finches. *Conservation Biology* 27(1):103–112. <https://doi.org/10.1111/j.1523-1739.2012.01944.x>

(2024) AntWeb. <https://www.antweb.org/>. Accessed 28 Mar 2024

Statements & Declarations

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Competing Interests

The authors have no relevant financial or non-financial interests to disclose.

Data availability

All data supporting the findings of this study are available upon request from the corresponding author.

Author Contributions

All authors contributed to the study's conception and design. Sample processing and data collection were performed by IJMB, ESGC, EBV, and GMRC. The taxonomic identification of invertebrates was conducted by IJMB, GMRC, ESGC, LBC, and ACR. GMRC performed the

statistical analyses. EBV, JMG, and GMRC obtained funding and resources for the study. The first draft of the manuscript was written by GMRC, and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

Tables

Table 1. Number of fecal pellets of lava lizards (*Microlophus* spp.) collected during this study by island, locality, and species.

		<i>M.</i> <i>albemarlensis</i>	<i>M.</i> <i>bivittatus</i>	<i>M.</i> <i>duncanensis</i>	<i>M.</i> <i>grayii</i>	<i>M.</i> <i>indefatigabilis</i>	<i>M.</i> <i>jacobi</i>	Total
Floreana	La Loberia				23			23
Isabela	Centro de Crianza	30						30
	Muro de Lágrimas	10						10
Pinzón	Playa Escondida			12				12
San Cristóbal	Centro de Interpretación		8					8
Santa Cruz	Garrapatero					30		30
	Tortuga Bay					37		37
Santiago	Playa Espumilla						27	27
		40	8	12	23	67	27	177

Table 2. List of food items, by order and family, identified from fecal pellets of each lava lizard species. For each lava lizard species, the number of occurrences of each food item and its relative frequency, calculated with the total of each *Microlophus* species, are shown between brackets.

Items are arranged in descending order of their relative frequency.

Order	Family	<i>M.</i> <i>albemarlensis</i>	<i>M.</i> <i>bivittatus</i>	<i>M.</i> <i>duncanensis</i>	<i>M. grayii</i>	<i>M.</i> <i>indefatigabilis</i>	<i>M. jacobi</i>	Total
Hymenoptera	Formicidae	107 (69.93)	31 (73.81)	21 (61.76)	51 (60.71)	333 (67.55)	68 (50.37)	611 (64.93)
Coleoptera	Unidentified	19 (12.42)	2 (4.76)	7 (20.59)	12 (14.29)	54 (10.95)	17 (12.59)	111 (11.80)
Hymenoptera	Unidentified	9 (5.88)	2 (4.76)	1 (2.94)	10 (11.90)	44 (8.92)	9 (6.67)	75 (7.97)
Hemiptera	Unidentified	3 (1.96)	1 (2.38)	2 (5.88)	4 (4.76)	17 (3.45)	11 (8.15)	38 (4.04)
Coleoptera	Curculionidae	2 (1.31)	0 (0.00)	0 (0.00)	3 (3.57)	22 (4.46)	1 (0.74)	28 (2.98)
Plantae*	Unidentified	4 (2.61)	3 (7.14)	2 (5.88)	0 (0.00)	7 (1.42)	11 (8.15)	27 (2.87)
Diptera	Unidentified	2 (1.31)	0 (0.00)	1 (2.94)	0 (0.00)	1 (0.20)	5 (3.70)	9 (0.96)
Coleoptera	Lucanidae	0 (0.00)	2 (4.76)	0 (0.00)	1 (1.19)	2 (0.41)	2 (1.48)	7 (0.74)
Lepidoptera	Unidentified	4 (2.61)	0 (0.00)	0 (0.00)	0 (0.00)	1 (0.20)	2 (1.48)	7 (0.74)
Odonata	Unidentified	0 (0.00)	0 (0.00)	0 (0.00)	0 (0.00)	7 (1.42)	0 (0.00)	7 (0.74)
Orthoptera	Unidentified	1 (0.65)	0 (0.00)	0 (0.00)	2 (2.38)	0 (0.00)	4 (2.96)	7 (0.74)
Psocodea	Unidentified	0 (0.00)	1 (2.38)	0 (0.00)	1 (1.19)	0 (0.00)	2 (1.48)	4 (0.43)
Araneae	Salticidae	0 (0.00)	0 (0.00)	0 (0.00)	0 (0.00)	1 (0.20)	1 (0.74)	2 (0.21)
Blattodea	Unidentified	1 (0.65)	0 (0.00)	0 (0.00)	0 (0.00)	1 (0.20)	0 (0.00)	2 (0.21)
Iguania*	Molt	0 (0.00)	0 (0.00)	0 (0.00)	0 (0.00)	0 (0.00)	2 (1.48)	2 (0.21)
Acari*	Unidentified	0 (0.00)	0 (0.00)	0 (0.00)	0 (0.00)	1 (0.20)	0 (0.00)	1 (0.11)
Coleoptera	Coccinellidae	0 (0.00)	0 (0.00)	0 (0.00)	0 (0.00)	1 (0.20)	0 (0.00)	1 (0.11)
Hymenoptera	Apidae	1 (0.65)	0 (0.00)	0 (0.00)	0 (0.00)	0 (0.00)	0 (0.00)	1 (0.11)
Mantodea	Unidentified	0 (0.00)	0 (0.00)	0 (0.00)	0 (0.00)	1 (0.20)	0 (0.00)	1 (0.11)
	Total	153 (100.00)	42 (100.00)	34 (100.00)	84 (100.00)	493 (100.00)	135 (100.00)	941 (100.00)

*While most were insects, some records include non-insect items outside this taxonomic classification (i.e., plant material, spiders, mites, and lizard skin molts).

Table 3. Number of ant individuals (relative abundance) detected in the fecal pellets of Galápagos lava lizards (*Microlophus* spp.) classified by subfamily. Note that most items correspond to introduced ant species (denoted by an *).

Subfamily	Ant species	<i>M.</i> <i>albemarlensis</i>	<i>M.</i> <i>bivittatus</i>	<i>M.</i> <i>duncanensis</i>	<i>M.</i> <i>grayii</i>	<i>M.</i> <i>indefatigabilis</i>	<i>M.</i> <i>jacobi</i>	Total Abundance
Dolichoderinae	<i>Tapinoma melanocephalum</i> *	85	13	0	20	2525	23	2666
Formicinae	<i>Brachymyrmex</i> sp1	6	0	0	0	40	2	48
	<i>Camponotus planus</i>	0	0	1	0	1	0	2
	<i>Camponotus</i> sp3	0	0	0	12	22	3	37
	<i>Camponotus zonatus</i> *	50	11	19	10	296	10	396
	<i>Nylanderia steinheili</i> *	0	3	10	2	43	17	75
	<i>Paratrechina longicornis</i> *	258	18	0	47	585	3	911
Myrmicinae	<i>Crematogaster</i> sp1	0	60	0	0	0	0	60
	<i>Cyphomyrmex</i> sp1	0	0	0	0	1	0	1
	<i>Monomorium floricola</i> *	21	13	4	5	326	15	384
	<i>Pheidole</i> sp1	1	0	0	0	0	0	1
	<i>Solenopsis geminata</i> *	0	1	5	9	8	14	37
	<i>Solenopsis globularia</i> *	6	0	0	13	4	1	24
	<i>Solenopsis</i> spp	15	52	0	1	73	117	258
	<i>Tetramorium lucayanum</i> *	0	0	0	0	0	6	6
	<i>Tetramorium</i> sp1*	6	0	6	39	63	116	230
	<i>Tetramorium</i> sp2*	0	0	0	5	13	0	18
	<i>Tetramorium</i> spp*	50	0	141	57	186	292	726
	<i>Wasmannia auropunctata</i> *	42	0	0	0	7	1	50
Ponerinae	<i>Odontomachus bauri</i> *	10	3	0	0	87	0	100
Unknown		260	0	0	1	80	4	345
	Total Abundance	810	174	186	221	4360	624	6375

Supplementary Material

Table S1. List of ant species present in the Galápagos Islands. Based on Herrera et al. 2024 and the sources therein.

Subfamily	Genus	Species	Status	
Dolichoderinae	<i>Dorymyrmex</i>	<i>D. pyramicus albemarlensis</i>	Endemic	
	<i>Tapinoma</i>	<i>T. melanocephalum</i>	Introduced	
		<i>T. sp. hh07</i>	Undetermined origin	
Dorylinae	<i>Cylindromyrmex</i>	<i>C. whymperi</i>	Introduced	
Formicinae	<i>Brachymyrmex</i>	<i>B. heeri</i>	Introduced	
		<i>C. macilentus</i>	Endemic	
	<i>Nylanderia</i>	<i>C. planus</i>	Endemic	
		<i>C. zonatus</i>	Introduced	
		<i>N. fulva nesiotis</i>	Introduced	
		<i>N. guatemalensis itinerans</i>	Introduced	
		<i>N. steinheili</i>	Introduced	
	<i>Paratrechina</i>	<i>N. vaga</i>	Introduced	
		<i>P. longicornis</i>	Introduced	
		Myrmicinae	<i>Adelomyrmex</i>	<i>Adelomyrmex longinoi</i>
	<i>Cardiocondyla</i>		<i>C. emeryi</i>	Introduced
<i>C. minutior</i>			Introduced	
<i>C. crinosa</i>			Uncertain	
<i>Crematogaster</i>	<i>C. JTL-022</i>		Introduced	
	<i>Cyphomyrmex</i>		<i>C. nesiotus</i>	Endemic?
<i>C. rimosus</i>			Introduced	
<i>C. sp. hh04</i>			Uncertain	
<i>Monomorium</i>	<i>M. cf. pharaonis</i>		Undetermined origin	
	<i>M. floricola</i>		Introduced	
	<i>M. pharaonis</i>		Introduced	
	<i>Pheidole</i>		<i>P. flavens</i>	Introduced
			<i>P. megacephala</i>	Introduced
<i>P. sp. hh01</i>			Undetermined origin	
<i>Rogeria</i>	<i>P. williamsi</i>		Endemic?	
	<i>R. curvipubens</i>	Introduced		
<i>Solenopsis</i>	<i>S. cf. basalis</i>	Uncertain		
	<i>S. geminata</i>	Introduced		
	<i>S. globularia</i>	Introduced		
	<i>S. gnoma</i>	Endemic?		
	<i>S. saevissima</i>	Uncertain		
<i>Strumygenis</i>	<i>S. eggersi</i>	Introduced		

		<i>S. emmae</i>	Introduced
		<i>S. luisianae</i>	Introduced
		<i>S. membranifera</i>	Introduced
	<i>Tetramorium</i>	<i>T. bicarinatum</i>	Introduced
		<i>T. caldarium</i>	Introduced
		<i>T. lacayanum</i>	Introduced
		<i>T. lanuginosum</i>	Introduced
		<i>T. simillimum</i>	Introduced
	<i>Trichomyrmex</i>	<i>T. destructor</i>	Introduced
	<i>Wasmannia</i>	<i>W. auropunctata</i>	Introduced
Ponerinae	<i>Hypoponera</i>	<i>H opaciceps</i>	Introduced
		<i>H. beebei</i>	Endemic?
		<i>H. cf. opacior</i>	Introduced
	<i>Leptogenys</i>	<i>L. santacruzii</i>	Endemic
		<i>L. sp. gorgona (hh03)</i>	Native
	<i>Odontomachus</i>	<i>O. bauri</i>	Introduced
		<i>O. ruginodis</i>	Introduced

Table S2. List of localities where lava lizard fecal pellets were collected for analysis during this study. The number of each locality corresponds with the numbers in Figure 1.

No.	Island	Locality	Latitude	Longitude	Elevation (masl)
1	Floreana	La Loberia	-1.280371	-90.489149	6
2	Isabela	Centro de Crianza "Arnaldo Tupiza Chamaidan"	-0.947471	-90.974072	15
3		Muro de Lagrimas	-0.964936	-91.012332	65
4	Pinzon	Playa Escondida	-0.599392	-90.654946	21
5	San Cristobal	Centro de Interpretacion	-0.890088	-89.609349	26
6	Santa Cruz	Playa El Garrapatero	-0.693715	-90.219377	5
7		Tortuga Bay	-0.758198	-90.330263	11
8	Santiago	Playa Espumilla	-0.203431	-90.82874	11

Table S3. List of food items identified in the fecal pellets of Galápagos lava lizards, detailing the total abundance of each and its relative frequency (in brackets). The relative frequency was calculated with the total abundance for each lava lizard species. The items with the maximum counts, and frequency, for each lava lizard species appear in bold.

Order	Family	Species	<i>M. albemarlensis</i>	<i>M. bivittatus</i>	<i>M. duncanensis</i>	<i>M. grayii</i>	<i>M. indefatigabilis</i>	<i>M. jacobi</i>
Acari	Unidentified	Unidentified	0 (0.00)	0 (0.00)	0 (0.00)	0 (0.00)	1 (0.02)	0 (0.00)
Araneae	Salticidae	Unidentified	0 (0.00)	0 (0.00)	0 (0.00)	0 (0.00)	1 (0.02)	1 (0.13)
Blattodea	Unidentified	Unidentified	1 (0.11)	0 (0.00)	0 (0.00)	0 (0.00)	1 (0.02)	0 (0.00)
Coleoptera	Coccinellidae	Unidentified	0 (0.00)	0 (0.00)	0 (0.00)	0 (0.00)	1 (0.02)	0 (0.00)
	Curculionidae	Unidentified	2 (0.22)	0 (0.00)	0 (0.00)	4 (1.47)	32 (0.68)	1 (0.13)
	Lucanidae	Unidentified	0 (0.00)	2 (0.96)	0 (0.00)	5 (1.83)	4 (0.08)	4 (0.53)
	Unidentified	Unidentified	40 (4.39)	19 (9.09)	14 (6.42)	18 (6.59)	130 (2.75)	31 (4.14)
Diptera	Unidentified	Unidentified	2 (0.22)	0 (0.00)	1 (0.46)	0 (0.00)	1 (0.02)	10 (1.34)
Hemiptera	Unidentified	Unidentified	3 (0.33)	3 (1.44)	3 (1.38)	4 (1.47)	26 (0.55)	24 (3.20)
Hymenoptera	Apidae	Meliponini	1 (0.11)	0 (0.00)	0 (0.00)	0 (0.00)	0 (0.00)	0 (0.00)
	Formicidae	<i>Brachymyrmex</i> sp1	6 (0.66)	0 (0.00)	0 (0.00)	0 (0.00)	40 (0.85)	2 (0.27)
		<i>Camponotus planus</i>	0 (0.00)	0 (0.00)	1 (0.46)	0 (0.00)	1 (0.02)	0 (0.00)
		<i>Camponotus</i> sp3	0 (0.00)	0 (0.00)	0 (0.00)	12 (4.40)	22 (0.47)	3 (0.40)
		<i>Camponotus zonatus</i>	50 (5.49)	11 (5.26)	19 (8.72)	10 (3.66)	296 (6.27)	10 (1.34)
		<i>Crematogaster</i> sp1	0 (0.00)	60 (28.71)	0 (0.00)	0 (0.00)	0 (0.00)	0 (0.00)
		<i>Cyphomyrmex</i> sp	0 (0.00)	0 (0.00)	0 (0.00)	0 (0.00)	1 (0.02)	0 (0.00)
		Unidentified	260 (28.54)	0 (0.00)	0 (0.00)	1 (0.37)	80 (1.69)	4 (0.53)
		<i>Monomorium floricola</i>	21 (2.31)	13 (6.22)	4 (1.83)	5 (1.83)	326 (6.90)	15 (2.00)
		<i>Nylanderia steinheili</i>	0 (0.00)	3 (1.44)	10 (4.59)	2 (0.73)	43 (0.91)	17 (2.27)
		<i>Odontomachus bauri</i>	10 (1.10)	3 (1.44)	0 (0.00)	0 (0.00)	87 (1.84)	0 (0.00)

		<i>Paratrechina longicornis</i>	258 (28.32)	18 (8.61)	0 (0.00)	47 (17.22)	585 (12.38)	3 (0.40)
		<i>Pheidole</i> sp	1 (0.11)	0 (0.00)	0 (0.00)	0 (0.00)	0 (0.00)	0 (0.00)
		<i>Solenopsis geminata</i>	0 (0.00)	1 (0.48)	5 (2.29)	9 (3.30)	8 (0.17)	14 (1.87)
		<i>Solenopsis globularia</i>	6 (0.66)	0 (0.00)	0 (0.00)	13 (4.76)	4 (0.08)	1 (0.13)
		<i>Solenopsis</i> spp	15 (1.65)	52 (24.88)	0 (0.00)	1 (0.37)	73 (1.55)	117 (15.62)
		<i>Tapinoma melanocephalum</i>	85 (9.33)	13 (6.22)	0 (0.00)	20 (7.33)	2525 (53.45)	23 (3.07)
		<i>Tetramorium lucayanum</i>	0 (0.00)	0 (0.00)	0 (0.00)	0 (0.00)	0 (0.00)	6 (0.80)
		<i>Tetramorium</i> sp1	6 (0.66)	0 (0.00)	6 (2.75)	39 (14.29)	63 (1.33)	116 (15.49)
		<i>Tetramorium</i> sp2	0 (0.00)	0 (0.00)	0 (0.00)	5 (1.83)	13 (0.28)	0 (0.00)
		<i>Tetramorium</i> spp	50 (5.49)	0 (0.00)	141 (64.68)	57 (20.88)	186 (3.94)	292 (38.99)
		<i>Wasmannia auropunctata</i>	42 (4.61)	0 (0.00)	0 (0.00)	0 (0.00)	7 (0.15)	1 (0.13)
	Unidentified	Unidentified	19 (2.09)	3 (1.44)	1 (0.46)	18 (6.59)	136 (2.88)	12 (1.60)
Iguania	Molt	Unidentified	0 (0.00)	0 (0.00)	0 (0.00)	0 (0.00)	0 (0.00)	2 (0.27)
Lepidoptera	Unidentified	Unidentified	13 (1.43)	0 (0.00)	0 (0.00)	0 (0.00)	1 (0.02)	8 (1.07)
Mantodea	Unidentified	Unidentified	0 (0.00)	0 (0.00)	0 (0.00)	0 (0.00)	1 (0.02)	0 (0.00)
Odonata	Unidentified	Unidentified	0 (0.00)	0 (0.00)	0 (0.00)	0 (0.00)	10 (0.21)	0 (0.00)
Orthoptera	Unidentified	Unidentified	1 (0.11)	0 (0.00)	0 (0.00)	2 (0.73)	0 (0.00)	5 (0.67)
Plantae	Unidentified	Unidentified	19 (2.09)	7 (3.35)	13 (5.96)	0 (0.00)	19 (0.40)	25 (3.34)
Psocodea	Unidentified	Unidentified	0 (0.00)	1 (0.48)	0 (0.00)	1 (0.37)	0 (0.00)	2 (0.27)
Total Abundance			911	209	218	273	4724	749

Figures



Fig 1 Map of the Galapagos lava lizards (*Microlophus* spp) sampling localities for this study. Main island names in the Galápagos Archipelago are displayed with reduced opacity, and each locality is denoted by white symbols. Floreana Island, 1 = La Lobería (*M. grayii*); Isabela Island, 2 = Centro de Crianza (*M. albemarlensis*), 3 = Muro de Lágrimas (*M. albemarlensis*); Pinzón Island, 4 = Playa Escondida (*M. duncanensis*); San Cristobal Island, 5 = Centro de Interpretación (*M. bivittatus*); Santa Cruz Island, 6 = Garrapatero (*M. indefatigabilis*), 7 = Tortuga Bay (*M. indefatigabilis*); Santiago Island, 8 = Playa Espumilla (*M. jacobi*). The frame surrounding the map denotes latitude and longitude with 0.5° divisions. Satellite imagery source: ESRI Satellite (ArcGIS/World_Imagery).

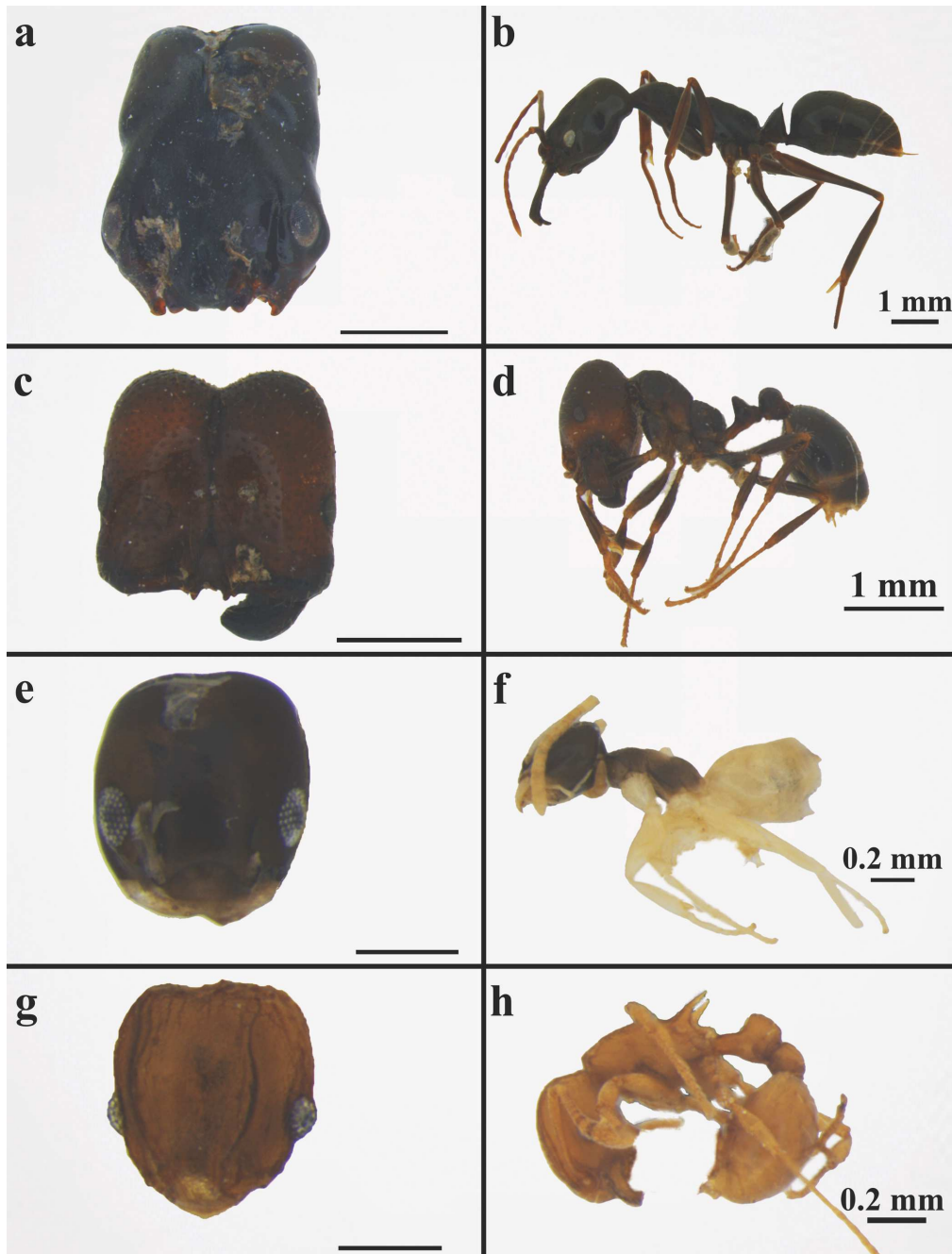


Fig 2 Photomicrographs of cephalic capsules (left column) from four introduced ant species identified in the fecal pellets of Galápagos lava lizards, shown alongside intact specimens for comparison (right column). **a & b** *Odontomachus bauri*; **c & d** *Solenopsis geminate*; **e & f** *Tapinoma melanocephalum*; **g & h** *Wasmannia auropunctata*. Cephalic capsules used for identification often lacked antennae or mandibles and were dislodged from the rest of the body, as illustrated in the left column images. Scale bar lengths for each species are indicated to the right of each row. Intact specimens on the right column were independently collected on San Cristobal Island for an unrelated study conducted by IJMB. Photos taken by IJMB.

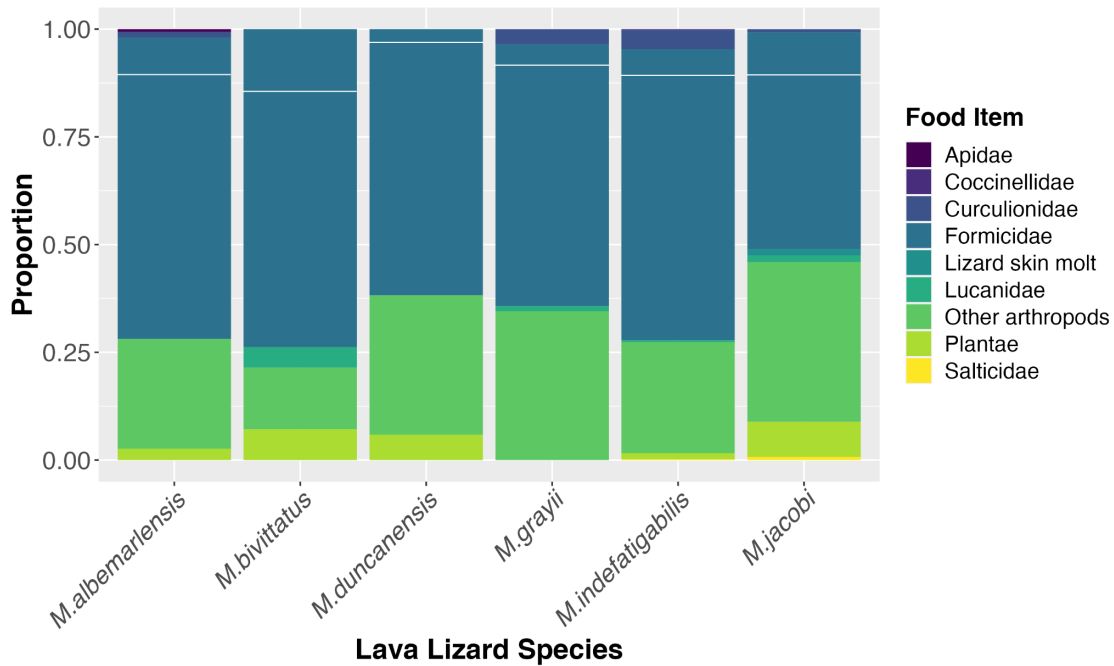


Fig 3 Relative proportions of dietary components in fecal samples from six species of Galápagos lava lizards based on the number of occurrences. Ants (Formicidae) are the predominant food item across all lava lizard species, constituting most of the diet. A horizontal white line within the "Formicidae" segment of each bar represents the proportion of introduced ant species relative to the total ant occurrences (*M. albemarlensis* = 87%, *M. bivittatus* = 81%, *M. duncanensis* = 95%, *M. grayii* = 92%, *M. indefatigabilis* = 91%, *M. jacobi* = 74%).

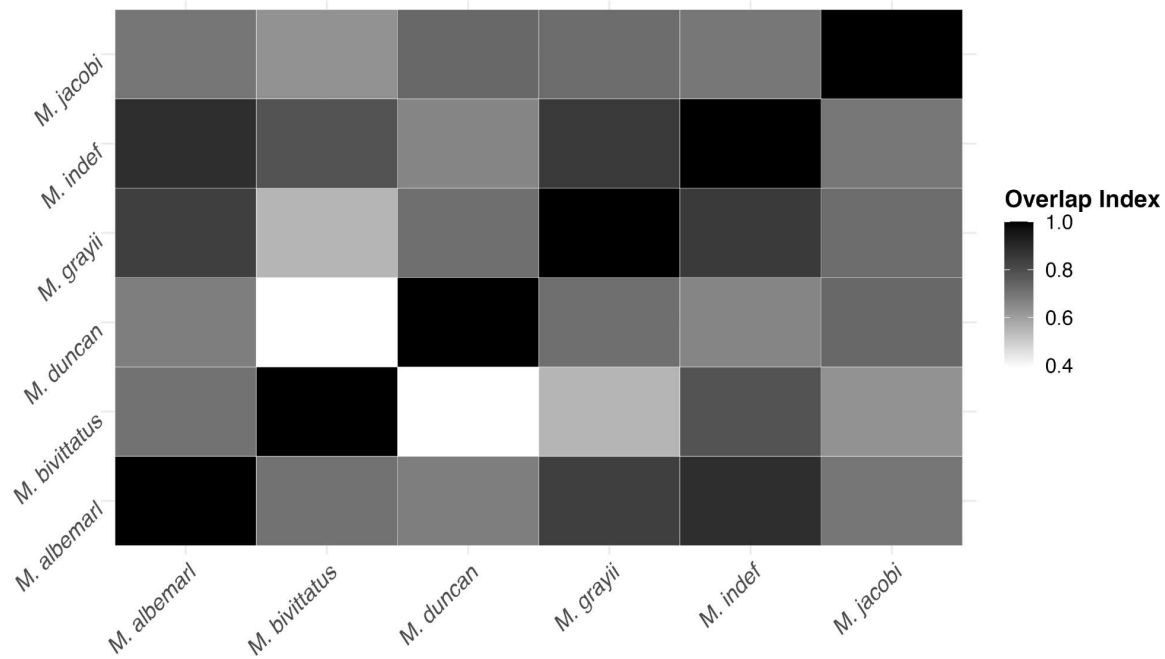


Fig 4 Heatmap showing the dietary overlap between the six Galápagos lava lizard species (*Microlophus* spp.) based on Pianka's overlap index. Each cell represents the overlap between the diets of two species, with color intensity indicating the degree of overlap—ranging from black (complete overlap, index value of 1) to white (no overlap, index value of 0). The highest overlap was found between *M. indefatigabilis* and *M. albemarlensis* (0.89) and, the least, between *M. duncanensis* and *M. bivittatus* (0.39).

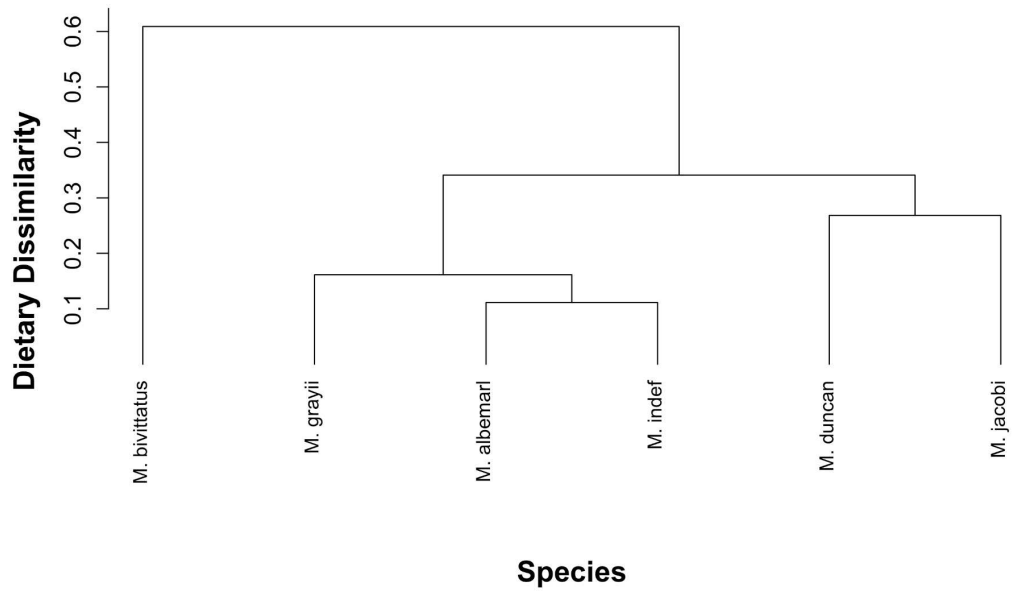


Fig 5 Hierarchical clustering dendrogram, based on the inverse Pianka's overlap index, showing the dietary dissimilarity among six species of Galápagos lava lizards (*Microlophus* spp.). Branch lengths on the vertical axis reflect the degree of dietary dissimilarity, with longer branches corresponding to bigger differences.

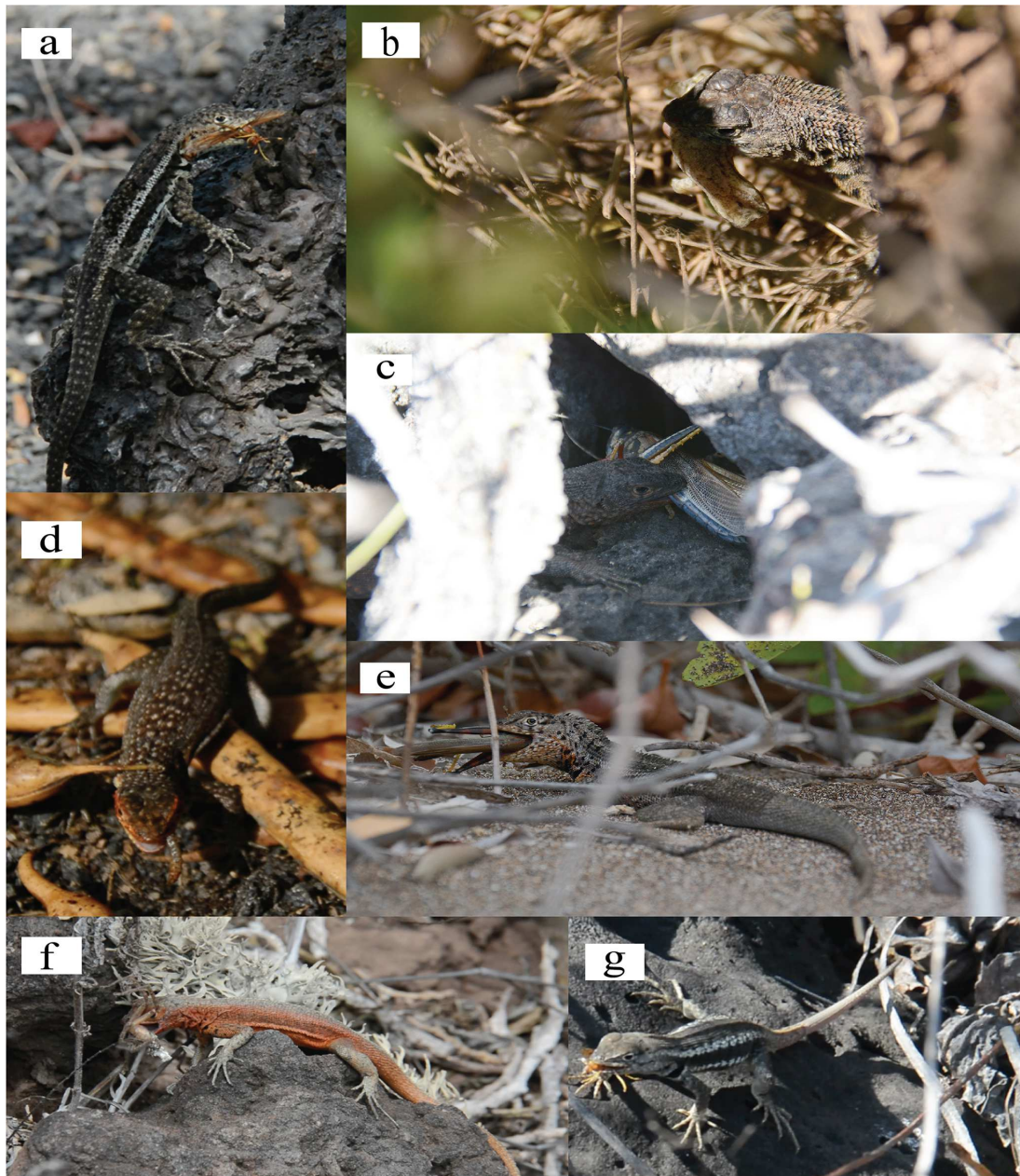


Fig 6 Photographic records of food items consumed by Galápagos lava lizards during fieldwork. **a.** A male of *M. bivittatus* eating a yellow paper wasp, *Polistes versicolor*. **b.** An introduced gecko, preyed by an *M. albermarlensis* male. **c.** A male of *M. duncanensis* feeding on an endemic grasshopper, *Schistocerca melanocera*. **d.** A female *M. albemarlensis* eating an earthworm from the soil. **e.** A male of *M. jacobii* consuming a grasshopper, *S. melanocera*. **f.** A female *M. duncanensis* eating a spider exuvia. **g.** A male *M. bivittatus* eating an unidentified wasp. Photos taken by ESGC.