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A Comparative Analysis of Gecko Toepad and Claw Morphologies, with regards to Body Weight, Locomotion and Habitat Occupancy.

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A Comparative Analysis of Gecko Toepad and Claw Morphologies, with regards to Body Weight, Locomotion and Habitat Occupancy.

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Declaration

I hereby declare that this thesis is the results of my own investigations, except where otherwise stated. All other sources are acknowledged by bibliographic references. This work has not previously been accepted in substance for any degree and is not being concurrently submitted in candidature for any degree unless, as agreed by the University, for approved dual awards.

Yr wyf drwy hyn yn datgan mai canlyniad fy ymchwil fy hun yw'r thesis hwn, ac eithrio lle nodir yn wahanol. Caiff ffynonellau eraill eu cydnabod gan droednodiadau yn rhoi cyfeiriadau eglur. Nid yw sylwedd y gwaith hwn wedi cael ei dderbyn o'r blaen ar gyfer unrhyw radd, ac nid yw'n cael ei gyflwyno ar yr un pryd mewn ymgeisiaeth am unrhyw radd oni bai ei fod, fel y cytunwyd gan y Brifysgol, am gymwysterau deuol cymeradwy.

Abstract

Gecko toepad and claw morphologies, claw presence/absence, body weight and general habitat type (Tree, Ground, Saxicolous and Multi), were compared against each other to find significant relationships. Although gecko morphology is widely varied, previous studies have limited toepad morphology to three groups and generalised their habitat occupation. This study analysed the different toepad morphologies of 153 species, creating six groups (toepad types) that detail the finer morphological distinctions between geckos' toepad types. Whilst also attempting to create an in-depth analysis of gecko habitat occupation, at the micro-level. A significant relationship was found between toepad morphology and habitat occupation, at the general level. A significant relationship was found between claw presence/absence and toepad type. Plus, significant relationships were found between 2 morphological claw characteristics (length and width) and toepad type. Body weight was analysed for 240 species, a significant relationship was seen with toepad type (151 species). Strong relationships were found between size corrected toepad and claw morphological characteristics, and body weight. Suggesting the need for further research, to determine the usefulness of these characteristics as predictors for gecko body weight. A small-scale Finite Element Analysis looked at claw morphology and structure from representative species of 5 of the 6 toepad types, from varying habitats, to determine the area(s) most susceptible to breakage due to stress. Interesting preliminary patterns were seen, revealing the need for a broader-scale study to better understand the finer complexities of gecko claw morphology and its potential relationship with habitat use. The results presented have highlighted the significant relationships between different morphological characteristics of geckos' claws and toepads, and the significant relationship(s) these traits have with each other and their habitat.

Acknowledgements

I would like to extend my sincere thanks to Dr. Kristen Crandell and Dr. Isabelle Winder for helping me to complete this thesis, especially in such unprecedented times. The patience and resolve that both of you showed to help this project be achieved, entirely via video calls, is truly appreciated. I am also grateful to Dr. Travis Hagey for providing the morphological images that allowed me to produce much more in-depth analyses than what was possible without them. Thank you all for your time and effort, it did not go unnoticed and will not be forgotten.

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Aims and Objectives

Chapter 1:

Aims:

In depth knowledge of geckos' natural microhabitat occupation and its relation to toepad morphology is scarce. The aim of this study was to discover any links between geckos' toepad morphology and their habitat occupation, at the general (e.g., forest) and micro (e.g., leaf litter) level. To see any potential morphological adaptations to living in their respective environments, at the microhabitat level. Plus, the adaptability of certain toepad morphologies that would allow certain species of gecko to live successfully in multiple habitat types.

No broad scale comparison of gecko species' body weight in relation to toepad morphology and therefore capacity for arboreality, has been conducted. The aim of the study was to discover any relationship between toepad morphology and body weight. To potentially uncover any morphological adaptations of the toepad that allow heavier geckos to maintain arboreality using the adhesive toepad system.

A large-scale comparison of gecko species' claw morphology and claw presence/absence and its links to locomotion has not been produced. The aim of this study was to uncover any relationship between geckos' claw morphology and/or claw presence/absence and their toepad type (i.e., adhesive, or non-adhesive). As this could show the physiological relationship between claws and the various adhesive and non-adhesive toepad types. Whilst also showing any possible trends in claw absence in relation to toepad type.

Objective:

- Collect the data via a search of the current literature.
- Collect scientifically accurate toepad images from a reputable source (Dr. Travis Hagey).
- Compile general habitat data into smaller more accurate microhabitat groups.
- Group toepads via morphology and adhesive capability, through image analysis.
- Analyse the claw images using ImageJ to collect morphometric data e.g., claw length.
- Analyse the claw images using ImageJ to note their presence/absence.

Chapter 2:

Aim:

A small-scale Finite Element Analysis of gecko claw structure would act as a source of preliminary data for future broad-scale studies into the links between claw morphology and strength, and habitat occupation. The aim of this study was to discover if there was any preliminary links to be seen between claw morphology and toepad type. Plus, claw morphology and the general (e.g., forest) and micro (e.g., leaf litter) habitats used by different gecko species. Whilst also uncovering whether claws can help compensate for a larger body weight in arboreal geckos, by providing additional support due to their strength and structure?

Objective:

- Choose representative species for each toepad type, that are also found in varying habitat types.
- Analyse the claw images using Finite Element Analysis software to create two-dimensional contour maps of the claws.
- Use the contour maps to determine the strongest and weakest point of each species' claw.

Introduction

Background

The suborder Gekkota contains six families, with a species count of more than 1500 (Zug, 2020). Gecko morphology varies greatly from their body size, ≤0.3g to ≥475g (Feldman *et al.,* 2016), to their claws, straight or curved, present or absent, and toepads: adhesive or non-adhesive. Their ecological adaptability is impressive in that they are found on all continents, excluding Antarctica. Gecko ecology, like morphology, is wide ranging. Habitat occupancy ranges from deserts to rainforests, with many species now found living in urban areas, in close proximity to people (Singh & Choudhury, 2016). This taxon's large species count allows for habitat and morphological variance to be examined in relation to ecological performance on different substrates. Specifically, scientists have yet to establish how claw and toepad morphology impacts gecko performance on a specific substrate, either positively or negatively. Typically, geckos are broadly categorised into two groups: arboreal and ground dwelling. This categorisation is based on their toepads, in that they are either adhesive or non-adhesive (Higham *et al.,* 2015: Gamble *et al.,* 2012); more arboreality can be achieved with adhesive toepads than without (Zaaf *et al.,* 2001). This thesis will aim to discover the relationships, if any, between morphological variation of geckos' claws (if present) and their function, their toepad shape and adhesion along with habitat use. Whilst also considering body weight as a possible factor behind these varying morphologies.

Adhesive Toepads: Structure, Loss/Gain and Morphology

Adhesive toepads are structures found on the base of the toes of arboreal geckos, they are absent from ground dwelling species. They are formed from branched seta, which are comprised of beta keratin protein (Liu *et al.,* 2015). The gene expression of beta keratins is positively correlated with seta formation in toepads of geckos (ibid.). Setae are rows of branched, hair-like structures, on modified scales known as lamellae (Ambrose *et al*., 2019). The individual setae are packed together tightly to form these rows (ibid.). Each individual seta branches off at the tip into even finer hair-like structures called spatulae (ibid.). The branched setae allow geckos to cling to surfaces through van der Waals forces (ibid.). These forces are weak individually, but when in the vast quantity as they are on geckos' feet, they can support a gecko's weight; for some, like the crested gecko, even when climbing upended (ibid.). This is because setae have high isoelectric forces and positive charges, which allow for stronger and more stable van der Waal bonds (Liu *et al.,* 2015).

Throughout their evolutionary history, the adhesive toepad system in geckos has frequently been gained and lost and sometimes gained again. It is approximated that adhesive toepads have been gained eleven times and lost nine times (Gamble *et al.,* 2012). Whilst the external adhesive structure is lost in some lineages of gecko - those that are ground dwelling - the internal biological structure, within the now non-adhesive toepad, remains (ibid.). However, this system is reduced in size (ibid.). This depicts that the capacity for gaining an adhesive toepad system again, is not truly lost (ibid.). The evolutionary reasoning behind the gain and, in some species, loss of adhesive toepads is an area of research that is currently ripe for more in-depth study. Another significant finding from Gamble *et al.* (2012) is the evidence of evolutionary transition between adhesive toepad types.

Toepads are broadly categorised into two groups: basal and leaf-like (Gamble *et al.,* 2012). Basal toepads have an adhesive system across the entire surface area of the base of the toe, whereas leaf-like toepads only have an adhesive system at the distal end of the base of the toe. Leaf-like toepads (Fig. 1) are also seemingly divided in two, vertically, creating two mirror-image 'leaf-like' structures.

Figure 1: An image of a representative species of gecko (*Strophurus ciliaris*) categorised as having leaf-like toepads.

The phylogenetic links between gecko lineages shows that leaf-like toepads derived either from ancestors without an adhesive system or from a basal adhesive system (which also derived from a lack of an adhesive system) (Gamble *et al.,* 2012: Russell and Gamble, 2019). This leads to interest regarding the significance of this evolutionary transition, and the need to further understand the mechanical effectiveness of both toepad types and if this effects their evolutionary selection.

Toepad Morphology and Habitat Occupation

Previous studies suggest that toepad morphology is linked to habitat occupation. Geckos with an adhesive system tend to exhibit a more arboreal lifestyle; and those without, are categorised as ground dwelling (Collins *et al.,* 2015). Ground dwelling geckos, like *Eublepharis macularius,* lack adhesive toepads, meaning that their climbing ability is limited to what can be achieved given their claw morphology (Jepsen, 2011). Whereas arboreal geckos, such as *Correlophus ciliates* possess adhesive toepads, allowing them to successfully climb various substrates (e.g., tree trunks, leaves and branches) and inclines (Zaaf *et al.,* 2001). There are links between gecko habitat occupation and performance, i.e., geckos appear to occupy the habitats that they perform best in, given their toepad and claw morphology (Pillai *et al.* 2020a). An example of this is the different microhabitat occupation of two gecko species living on the same island (Giraglia Island, Corsica) (Russell and Delaugerre, 2016). Both gecko species possess adhesive toepads, however *Euleptes europaea* has leaf-life toepads and *Tarentola mauritanica* has basal toepads. *Euleptes* prefers the more natural, saxicolous environments, compared to *Tarentola* which is restricted to one concrete building on the island. It is suggested that as leaf like toepads can be lifted from the ground, such that only the claw is in contact with the substrate, the dust in the natural, rocky habitat cannot affect the setae of *Euleptes* and their self-cleaning mechanism. This allows *Euleptes* to rely solely on its claws when in this environment. Geckos with basal toepads cannot do this, meaning their setae would be inhibited from self-cleaning almost immediately, due to the dust within the saxicolous environment. This limits *Tarentola*'s environment to the flatter, dust-free man-made building. This shows clear microhabitat restriction that leads to niche fulfilment, in accordance with morphology, specifically of the toepads. To test if there are more examples of niche fulfilment like this across all geckos, more information would be needed regarding geckos' microhabitat occupation, along with their toepad type and their location.

Toepad Clinging Performance

Some studies link changes in some gecko species' clinging performance to differences in substrate, across varying degrees of surface roughness, showing how microtopographies can influence clinging performance. However, in many instances, the substrates used were artificial. One study of *Pseudothecadactylus australis* and *Oedura coggeri* showed no significant difference in clinging performance between the substrate with the smoothest surface and the substrate with the roughest surface (Pillai *et al.*, 2020b). Using samples of the substrates in the geckos' natural environment may have led to different, more significant results, which is why information on microhabitat is needed, to test this assumption. There are also findings that characterise the speed constraints that come with having an adhesive toepad system. This impacts on the geckos' predator evasion behaviour, which in turn, impacts their habitat occupation as natural selection would confer benefits on individuals that occupy an environment with the substrates that allows them to evade predators most efficiently (Collins *et al.,* 2015). When the geckos no longer solely rely on their claws (if they have any) for clinging to the substrate, findings suggest that the deployment of the adhesive system can be linked to gravity i.e., the angle of the incline (Russell and Higham, 2009). This differs from previous assumptions that surface roughness determined when the adhesive system was deployed (ibid.).

Humidity also needs to be considered when discussing the gecko habitats and locomotor performance. Several studies have been conducted investigating the effects of humidity on the adhesion performance of toepads. Niewiaroski *et al*. (2008) found that when temperature increases, clinging force decreases when relative humidity also decreases. However, when the temperature is stable at 12°C the clinging force exhibited by the toepads increases with humidity (up to 80% relative humidity). The same result was seen at 32°C. This suggests that the key factor in the adhesion clinging force exhibited by the two species of gecko in this study was humidity. The limitations of this study were that only two species were observed, the substrate was artificial and both species were basally padded geckos. Puthoff *et al*. (2010) showed similar results in that adhesive clinging force also increased with relative humidity. Again, an artificial substrate was used and only on species that have basal pads. This is seen once more in a study conducted by Tao *et al.* (2015) using artificial substrates and only one gecko species. However, they discovered that when relative humidity is >40% the adhesion that the toepads are capable of becomes saturated when sliding, suggesting that there is a limit to the impact which increasing relative humidity can have on geckos' adhesive force. Because of these findings, it is important to factor in humidity when grouping habitat type as humidity may influence how arboreal geckos cling to the substrates in these environments. Only one toepad type was analysed in these studies, basally padded. Since there are at least 2 different adhesive toepad types it would be intriguing to ascertain if there is a link between toepad type and clinging performance, and habitat humidity. The geckos' general habitat would need to be considered in relation to their larger-scale geographical location, as this would allow for the collection of more relevant and accurate data regarding temperature and humidity, to look for any trends and/or relationships.

Habitat classification is what has limited the current literature's findings. This is because comparing gecko morphology within broad scale habitat types, e.g., forest and desert, does not account for the potential finer morphological differences between gecko species, that use different habitats, at the microhabitat level. A study conducted by Riedel *et al.*, (2020) showed the differences in locomotion type and perch height as well as the humidity level of the microhabitats occupied by 34 species of Australian geckos. Therefore, more definitive information about, and classification of, gecko microhabitats is needed to gather, and will allow for a more detailed morphological comparison that could show the subtle, yet potentially significant, differences between toepad morphology and clinging performance; by considering links, if any, to surface roughness of the substrate(s) in use. These characters are in addition to known incline angles and, specifically with arboreal geckos, their preferred dwelling height (Kim *et al.,* 2018). A variable to also factor in when discussing morphology and habitat choice is body size and weight. As this will significantly

affect locomotive performance and clinging capabilities; either via claws and/or adhesive toepads (Labonte and Federle, 2015: Russell and Johnson, 2014). Which would help to discover the finer details of gecko locomotion, e.g., how the claws and toepads contribute either individually or together, to adhesion and/or locomotion. Therefore, discovering whether toepad and claw morphology is correlated with habitat occupation could help to further understand the how and why behind geckos' locomotion.

Body Weight and Adhesivity

Geckos are the heaviest animals that climb using an adhesive system. It is indicated that some exceed the upper limits of size for equal load sharing (Labonte and Federle, 2015). Equal load sharing is the when the shear forces are shared across the surface of the toepads, equally. Gilman *et al*. (2015) also note that there is a large scaling difference in body weight and size of arboreal geckos, up to 150 times. Gravish *et al*. (2009) discusses how contact force between the setae and the substrate increases as shear forces displace the setae and initiate adhesion. These are known as "stick-slip events" because the gecko lands on a substrate, and is momentarily sticking to said surface, shear forces then impact upon the gecko, and it begins to slip. Resulting in an increase in contact force, leading to adhesion. This does not require the load sharing to be equal, which could help explain how geckos of a larger body weight are able to maintain surface contact, since the contact forces between the setae and the substrate increase as shear force increases. A larger body weight would help increase their shear force when 'slipping'. In relation to mass, lighter geckos produce overall higher shear forces than larger geckos, as they have a higher surface-to-volume ratio (Russell and Johnson, 2014). The gecko adhesive toepad system, across sizes, generates more adhesive force than what is needed to support the gecko's body weight; known as its safety factor (ibid.). Larger geckos typically have larger toepads, therefore larger overall attachment forces. However, the larger the gecko the smaller their safety factor becomes due to their smaller surface-to-volume ratio (ibid.). Larger geckos' reduced safety factor is most likely compensated for by the previously explained mechanisms that occur during "stick-slip events" (Gravish *et al.,* 2009: Russell and Johnson, 2014).

Russell and Johnson (2014) and Labonte *et al.* (2016) found that toepad size scales isometrically rather than allometrically, after a given body size. The reasoning for this is that toepads can only grow so large before each individual pad would begin to overlap the other(s) at its side(s). This would mean they attached to each other and compromise the gecko's locomotive capacity, effectively becoming functionally useless. These authors also showed that larger toepads do not compensate for a larger body size, and that body size and weight are morphological constraints that effect geckos' overall clinging performance. This leads to the question of how larger geckos have evolutionarily adapted their morphology to compensate for their size and continue living arboreally. Is there a relationship between an adhesive toepad type and body weight? Is it linked to the number of lamellae on said adhesive toepad type, and body weight? Other factors that affect clinging performance, in addition to toepad type, is setae, therefore lamellae, formation and location. Labonte and Federle (2015) discovered that one species of gecko, *Chondrodactylus bibronii,* displayed a variance in setae formation correlating positively with body weight. Whilst the density and diameter of the setae remained the same in all individuals, setae length had increased with body size, intraspecifically. This indicates a possible physical adaptation to the constraints of a heavier body weight, allowing the continued arboreal lifestyle of the species.

These findings show that there is much still unknown about how body size, specifically body weight, effects the climbing performance of arboreal geckos. This leads to question whether the loss of the adhesive system in ground dwelling species of gecko was because of body size and weight, or something else. We assume that, after a given body weight, the animal would become too heavy to be able to physically support itself arboreally, using adhesion. Therefore, it would be expected to evolutionarily change its morphology, losing the adhesivity of its toepads, and adapt to a ground dwelling lifestyle. Plus, more information is needed at the setae level, regarding the

subtleties of local adjustment. A change in setae, and therefore lamellae, position within different toepad types could explain a difference in adhesive toepad types for some species (Russell and Johnson, 2014).

The efficiency of the different toepad types (basal and leaf-like) and their mechanisms are largely unclear and need further investigation. Labonte *et al.* (2016) suggests that the evolutionary reasoning behind changes in adhesive toepad morphologies, whether they have been lost or gained, is likely down to ecology (i.e. niche fulfilment) and behaviour. Often there is a trade-off between adhesivity and arboreality, and locomotor performance at times when adhesivity is not needed. For example, when fleeing a predator on the ground, the morphology of the legs plus the adhesivity of the toepads could slow the animal, therefore increasing its risk of predation. This is why it is logical to assume that habitat and behaviour are factors in the ecophysiological changes exhibited by geckos over evolutionary time. Given the taxonomic diversity within the Gekkota suborder, it is a difficult task collecting the necessary morphological data needed to definitively ascertain what the functional purpose of these differences (body weight and toepad type) are. This is why more research is needed, and this study is being carried out. One goal of this research, as stated at the outset, is therefore to discover links, if any, between the morphological characteristics of gecko toepads and their habitat use. It will also explore whether toepad width or type has any overall influence on gecko microhabitat occupation, as was shown in the Giraglia Island example of different ecological niches being fulfilled and microhabitats being occupied, based on toepad morphology (Russell and Delaugerre, 2016). It will also be important to see whether the number of lamellae present on geckos with adhesive toepads is linked to pad type and/or body weight and/or microhabitat, given the previously explained information on how body weight effects shear force and clinging performance (Labonte and Federle, 2015: Gravish *et al*., 2009).

Claw Structure

Evolutionary changes in claw structure have permitted geckos to possess an array of claw shapes and sizes. Claws are comprised of laterally compressed keratin which grows outwards from the end of the digit, forming the base of the claw and creating the pointed, curved structures (Kardong, 2009). Therefore, the dorsal side of the claw, known as the unguis, has become a modification of the outer scale, which was formerly at the end of the digit (Alibardi, 2009). The biological structure of the reptilian claw varies significantly from that of mammals. The mammalian claw has localised cell proliferation in the matrix of the claw (ibid.). These cells are responsible for claw growth and are located at the base (ibid.). The reptilian claw possesses these same dividing, growth cells; however, they are distributed evenly across the epidermis from the proximal base, to the tip (ibid.). The ventral side of the claw is known as the subunguis and is a softer structure created to support the claw from its underside (Kardong, 2009).

Claw Morphology and Loss

Interestingly, geckos are the suborder with the highest rate of claw reduction and/or total loss among the lineages of normal limbed lizards (Russell & Bauer, 2008). The *Tarentola* genus of geckos is noted for having a large amount of its species with a reduction in the number of digits with claws, whilst some species have lost their claws altogether (Khannoon *et al.,* 2015). This genus typically has large claws on digits III and IV with partial and/or total claw loss on digits I, II and V. The claw loss is associated with apoptosis, which is a biological process that occurs in cells, known as programmed cell death. Apoptosis occurs during embryonic development (Anon, 2020) for the *Tarentola* genus. Therefore, this process of programmed cell death, has already taken effect before there are any notable signs of claw formation. Meaning that the species exhibiting claw loss still possess the genes for claw formation. However, these genes are over-ridden by others that drive claw loss during development (Khannoon *et al.,* 2015).

Given the noted differences in the number of claws different gecko species possess, understanding their role in a gecko's locomotor performance and behaviour is crucial as this will lead to a better understanding of geckos' ecological presence, in various habitat types. Zani (2000) discovered that evolutionary increases in claw curvature, adhesive toepad size and lamellae number, all contribute to an increase in lizards' clinging performance on smooth surfaces. This includes geckos, for whom an increase in claw height, and claw curvature, along with a decrease in digit length all aid in an increased clinging performance on rough surfaces (ibid.). Therefore, these morphological changes correlate with evolutionary changes that lead to an increased clinging capacity, which is seen in arboreal geckos. A study conducted by Dai *et al*. (2002) shows an increase in friction force between beetle claws and the substrate, when surface roughness of the substrate is larger than the diameter of the claw tip. This implies that sharpness plays a key role in grip, and therefore in climbing ability for said beetles (*Pachnoda marginata*) on different surfaces and suggests that topography, therefore microhabitat, influences climbing and clinging performance. Birn-Jeffery *et al*. (2012) linked claw shape to behaviour of extant birds and lizards that are 'ground-dwellers', noting that their claws shape is typically straighter and deeper, dorsoventrally, compared to species in other behavioural categories. This study noted however, that a lack of specification regarding the ecological categories in other studies, makes linking claw shape to lifestyle/behaviour difficult, with seemingly no detectable pattern/relationship. It therefore highlights the significant need for further research linking morphology and ecology, at the more specific microhabitat level.

Naylor and Higham (2019) learned that when geckos' claws were partially and/or fully removed, the clinging force exhibited by the geckos with adhesive toepads and claws, on both rougher and softer (non-acrylic) surfaces, at high inclines, decreased. Depicting that geckos rely on their claws for clinging to rougher surfaces and their toepads for clinging to smoother surfaces; in this study the smoother surface was acrylic. However, partial, or full removal of claws had relatively little effect on arboreal geckos' clinging force, at lower inclines. These discoveries, along with the knowledge of evolutionary claw loss in some species, leads to the need for better understanding the functional role of claws, regarding gecko locomotive performance. This could be achieved with more in-depth habitat knowledge at the micro level, as knowing what natural substrates, and therefore natural topographies, geckos encounter in their natural environment(s), could uncover the reasoning for the evolutionary morphological changes in claw shape, size and presence.

Claw Functionality Alongside Adhesive Toepads

Partial and/or total claw loss has only been observed in gecko species that possess an adhesive toepad system, indicating that claws play an important role in ground dwelling geckos' locomotion. Whereas, for some species of arboreal geckos their claws are presumed to be functionally redundant for their locomotive style and have therefore been lost over evolutionary timescales (Naylor & Higham, 2019) Some gecko species that are lacking an adhesive toepad system, those that are ground dwelling, have been noted to have lost their adhesive system as they underwent a change in habitat type. There are two genera of geckos, *Pachydactylus* and *Chondrodactylus* that have seemingly evolutionarily lost their adhesive system when their habitat occupation changed from saxicolous environments to burrowing in loose sand (Gamble *et al.,* 2012). This therefore reiterates the theory of functional morphological changes in claw and toepad morphology to adapt geckos to occupy different ecological niches.

Studies conducted on the *Anolis* genus of lizards provide some insight into how claws aid in locomotive performance. Anole lizards are similar to geckos in that they also possess adhesive toepads (Hagey et al., 2017) and vary in size and weight between species. Current studies show a difference in claw morphology in those species that are arboreal compared to species that are ground dwelling and suggest that their adhesive toepads and claws co-evolved to adapt to differing habitats (Crandell *et al.,* 2014). In addition, Yuan *et al*. (2019) discovered that the rates of evolution between claws and adhesive toepads are an example of adaptive phenotypic traits allowing arboreal anoles to occupy more microhabitats, fulfilling more ecological niches than species lacking

adhesive toepads. This is evident given that claw height increased with perch diameter and that claw curvature was positively associated with perch height. However, it was claw length that evolved at the fastest rate; even though its functional importance and purpose remains unclear. This conclusion reiterates the findings of Crandell et al. (2014), that functional morphology is a research area that needs further investigation. Given the findings of the current literature the need for further investigation into the adaptive functional role(s) of claws, regarding gecko locomotion and the links to habitat occupation, is unquestionable.

Summary

In summary, this comparative morphological study, which includes data on 240 species, will attempt to link the morphology of geckos' toepads and claws to their microhabitat occupation. By differentiating the gecko species via toepad type, adhesive or non-adhesive, and locomotive ability, arboreal or ground dwelling, and body weight, it will help discover if any relationships between these factors exist. It is hoped that this study will reveal the answers to some of the pressing questions regarding geckos' ecological adaptability.

Using photographs of live and museum specimens, claw presence/absence and measurements e.g., length, will be taken and compared against the geckos' toepad type and habitat to discover any trends/relationships that might be present. The study will also include a small-scale finite element analysis of the claws of example geckos of each locomotor type, to create contour maps of the claws. This will help to discover the strongest and weakest areas of their claws.

Hypotheses

My hypotheses for this study are as follows:

Arboreal geckos with leaf-like adhesive toepads will occupy a wider range of microhabitats than those with basal adhesive toepads. In the example given by Russell and Delaugerre (2016) of two gecko species observed on Giraglia Island, geckos with different toepad types occupied different habitat(s). The species with leaf-like toepads was observed occupying more habitat types than the basally padded gecko, which was only seen using one.

Body weight will factor in determining the geckos' capacity for arboreality, due to the upper size limits on equal load sharing across the adhesive toepad as well as the morphological size constraints on increasing the adhesive toepad size (Russell and Johnson 2014: Labonte *et al.* 2016: Labonte and Federle, 2015). *Therefore, geckos that are ground dwelling will, typically, be heavier than those that are arboreal.*

To test these hypotheses, for each gecko species their toepad type, body weight, and general and micro habitat information will be collected and compared to discover any trends or relationships that may be present. By comparing these categories and measurements against each other, the study will aim to better understand how gecko morphology and ecology relate to one another.

An increase in claw curvature will redirect forces to a single point along the claw (Manning et al., 2009), *reducing the area that is susceptible to breakage, to the tip. Allowing the rest of the claw to endure an increased stress load. This will be seen in arboreal geckos as they need an increase in claw strength to assist them when climbing vertically.*

An increase in claw curvature will be seen in geckos with an arboreal locomotive capacity, compared to those that are ground dwelling as these are known to have straighter claw shapes. This would fit with Birn-Jeffery *et al*. (2012)'s discoveries in their study on extant bird and lizard pedal claws.

Geckos that are arboreal will have a reduced claw size compared to those that are ground dwelling, as they can also rely on their adhesive toepads for climbing. As discussed by Russell and Gamble (2019), as pad-bearing geckos can lift their claws to procure a better purchase on the inclined substrate whilst using their adhesive toepads to uphold their grip.

Methodology

To meet the main goal of this study, it was first necessary to create a comprehensive dataset, as this would help to discover relationships between geckos' toepad and claw morphologies in addition to any relationships between them and habitat use, locomotion type and body weight. The comprehensive data set included morphological, locomotive, habitat and location information for a variety of gecko species (240). This data set was compiled through a thorough and comparative literature search of previous studies' findings regarding geckos' toepad and claw morphology as well as body weight. Alongside this, internet searches for geographical topographies of the general habitats, to discover more detail about the microhabitats that geckos occupy, was also carried out. Plus, a detailed image analysis of toepad and claw morphology was conducted, to categorise and measure toepad morphology, note claw presence/absence, and take morphological measurements. Finally, a finite element analysis was used to determine the points of strength and weakness for different claw shapes, by creating 2D contour maps to discover the areas of the claws under the lowest and highest amounts of stress.

Data Collection

A literature review was carried out to collect the necessary data for this study. Two principal papers were used as a basis, as one included a large species list with body weight data (Meiri, 2010), and the other contained a large species list with general habitat classifications (Kulyomini et al., 2019) (112 species). The data from these papers were merged to create one large dataset with both body weight data and general habitat information for each species. For any species remaining on the full list without body weight data, literature searches were done. This led to additional species being added to the full species list, if their body weight information was also present in the additional papers found (Appendix 1: Table 1), creating a list with 240 species in total. Where available, the body weight for each sex of each species was noted, along with if the body weight was the average or the heaviest. This allowed for sexual dimorphism to be considered if needed. However, it was ultimately decided that taking the average weight would be better, if more than one measurement was present as there were minimal differences in weight with those species that showed sexual dimorphism. To obtain an average, either one weight from each sex or a weight for one sex and an average for the species, were used to calculate the representative average for the species. If the weight measurement was from a larger individual, but no other weight information was available, then it was used as a representation for the species because at least this showed the upper size limit that an individual of that species could reach, whilst maintaining its natural behaviour/lifestyle.

Once the species list of 240 species was finalised and the body weight data collected, additional literature searches were made to find any published information regarding the species' microhabitat type and location. Location was searched for as, if no microhabitat data were available, then their location would be researched, via google searches for the geographical information that would help determine their environment and the topographies that they would encounter. For microhabitat data, the general habitat allocation system employed by Kulyomini et al. (2019), was used to classify the general habitat for those species not present in the Kulyomini et al. (2019) research paper. The microhabitat findings led to change in the general habitat classification for some species, if they were found in different/varying environments that contradicted the general habitat information. As the microhabitat data provided more specific information, I chose to change the general habitat classification of a species where the two types of habitat data did not match. General and microhabitat, location (Appendix 1, Table 2) and body weight data was collected for 240 species.

Data Grouping

Consistent data labelling was needed before any analysis could be ran. To do this, the microhabitat data was grouped into sub-categories using the General Habitat allocation system employed by Kulyomini *et al.* (2019) as a starting point, as detailed below.

Habitat

The General Habitat allocation system employed by Kulyomini et al. (2019), comprised of 4 groups: Tree, Saxicolous, Multi and Ground.

'Tree' species were sub categorised via the microhabitat data collected, creating 13 groups in two categories. This was to provide more accurate and detailed habitat information for each species of gecko, rather than simply placing them all under one general and highly varied category.

Category 1 was 'Forest', this was then separated into six groups by humidity and forest type:

- Tropical, Sub-Tropical and Coastal represent the humid environments.
- Deciduous, Coniferous and Tropical (Dry) represent the dry environments.

Category 2 was 'Vegetation', which was separated into seven further groups by type and density:

- Species Specific plants (i.e., found, almost exclusively, on or near specific species of vegetation), Forest Debris/Floor and Above Ground represent vegetation type.
- Agroforestry, Grassland, Shrubland, Heathland and Scrubland represent the vegetation density.

'Saxicolous' species were separated based on rock density/type or place on/within the rock(s) where the individual(s) were found.

- Urban, Semi-Desert, Outcrops, Specific Rock Types, Under/Within and Rock Surface.

'Multi' was not separated into any groups. Instead, all species in this category were placed in any group(s) that they fitted into. They therefore appeared in multiple data samples because these species occupied multiple habitat types.

'Ground' species were separated into five groups based on general ground type/condition which the individual(s) would regularly encounter/were found in:

- Sand, Hydric, Xeric - minimal vegetation, Mountains and Ground Debris.

Toepad Morphology

The toepad and claw images were collected from a source outside of Bangor University, Dr. Travis Hagey, who was willing to contribute data to this study. The images used were of museum specimens and live animals (Appendix 1, Table 3). These images enabled the collection of claw presence and locomotion type (Arboreal or Ground Dwelling) data, in addition to more accurate and in-depth information regarding toepad morphology. Toepad and claw images were analysed for 155 of the 240 species. Data was collected from an image of one specimen of each species.

Upon visual analysis of the toepad images (Fig. 2), it was clear that the variation in morphology was far wider than simply dividing the toepads into the standard two categories, Basal and Leaf-Like, which was done in previous studies (Gamble *et al.,* 2012). The toepads were therefore separated into six distinct groups (one of which was split into two sub-groups) I created based on my personal observations:

1. Basal – Toepads comprised of undivided lamellae across the entire toepad.
2. Leaf-Like – Toepads with 1 vertical division across the entire adhesive area of the toepad creating 2 distinct mirror-image adhesive pads, with notable non-adhesive spacing between.
3. Non-Adhesive – Toepads possessing no lamellae, therefore no adhesive capacity.
4. Paired Division – Toepads with 1 vertical division across the entire adhesive area of the toepad, along with multiple horizontal divisions, creating pairs of adhesive areas along the toepad.
    A. If pairs are round in shape (similar to leaf-like).
    B. If pairs are thinner and oblong in shape, with more condensed lamellae.
5. Partial Division – Toepads with 1 vertical division across the toepad, that leads to less prominent separation of adhesive area: from the tip of the pad to base.
6. Fanned – Toepads with 1 partial to full vertical division creating 2 ‘fan-like’ shaped adhesive pads. The lamellae either increased or decreased in length, from the tip of the pad to the base.

Figure 2: Example species of geckos with toepad type 1 (*Correlophus ciliatus*), 2 (*Phyllodactylus xanti*), 3 (*Carphodactylus laevis*), 4a (*Amalosia rhombifer*), 4b (*Bavayia cyclura*), 5 (*Thecadactylus rapicauda*) and 6 (*Ptyodactylus guttatus*).

The image analysis software ImageJ (Rasband and Contributors, 2021) was used to collect the measurement data from each toepad image. The fourth toe on either the left or right hind foot was used when doing this, for continuity. Each image was of an individual representative of each species. The measurements collected from each image (if present/possible) were the width of the toepad from the widest point (including the width of any divisions, if present), and the width of the vertical toepad division (if present), at the widest point. Finally, the number of lamellae were counted (if present/visible). To differentiate between lamellae and toe scales, care was taken to count from the middle of the underside of the toe, to ensure that no toe scales on the outer sides of the toes were counted as lamellae by mistake.

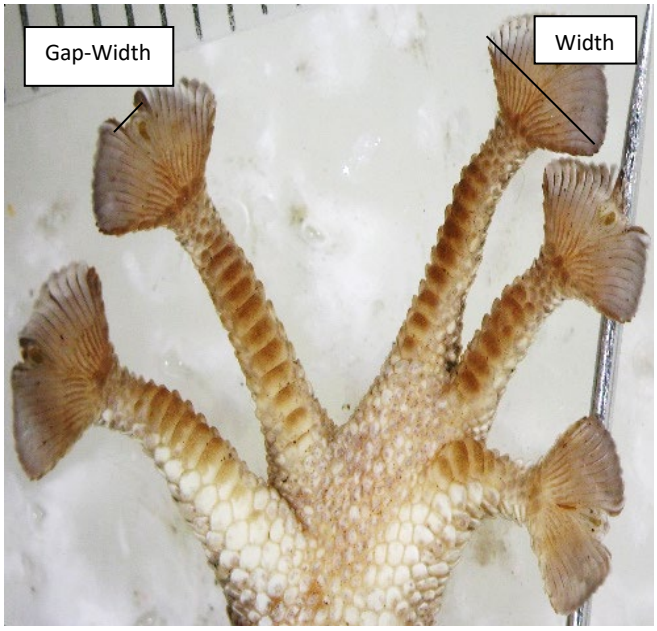

Figure 3: Representative image (*Ptyodactylus guttatus*) depicting how each morphological characteristic for the toepads were measured. Along with each individual lamellae on the toepad being counted, using the ImageJ software.

The scale for each image was set before any measurements were taken. Each image had a ruler present for scaling purposes. The scale was set using this ruler, through drawing a line over 5mm, to better correct for intra-observer error over using only 1mm. Then each of the aforementioned measurements were taken, sequentially. This was repeated thrice for the "Toepad Gap-Width" and "Toepad Width" measurements for all 143 species that I was able to acquire an image of, to attain an average that better corrected for intra-observer error. Also, by taking a different measurement to the previous, on the same specimen, each time, it meant that each new measurement was taken without the presumption that the first was correct. This minimised repeated errors through assumption and complacency (The University of North Carolina at Chapel Hill, n.d.). The lamellae were counted using the "Multi-Point" tool in ImageJ that assigned a number to each mouse click, therefore assisting in the counting, reducing the chance of miscounts. This approach meant the number of lamellae only needed to be measured once, not three times like the other two toepad measurements. Once all the measurement data was collected a repeated measures test was carried out by calculating the mean and standard deviation for each set of three measurements. Dividing the standard deviation by the average allowed for the calculation of the percentage of difference, between the measurements, scaled with the overall size of the measured trait. If higher than 5%

then the measurements would be re-taken until a set of three new measurements had a standard deviation of 5% or less. Only ≤15 species required repeated measures.

Claws

Each toepad image was visually analysed for claw presence/absence. The number of claws present for each species was recorded, along with their digit location. If the species possessed any visible claws, they were recorded as having claw presence. If no claws were visually present the species was deemed as being absent of claws. However, it was noted that the claw loss could be down to individual specimen loss and not a species wide trait, and that further study would be needed to determine the true cause of the claw loss. Again, the image analysis software ImageJ was used to collect the measurement data for the claws from the same set of images. The measurements collected from each image (if present/possible) were claw length, which was straight across from tip to base to measure the direct length of the claw; claw width, which was straight down from the highest point of the curve to the underside of the claw and claw height, which was straight down from the dorsal to the ventral side of the base of the claw (Fig.4). Lastly, I measured claw curvature (Fig. 5).

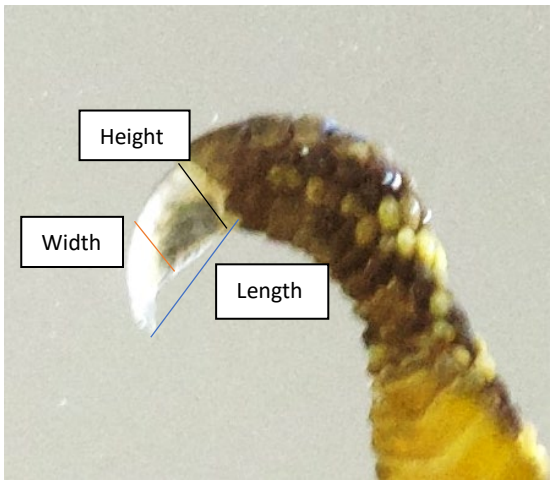

Figure 4: Representative image (*Mokopirirakau granulatus*) of how each claw measurement (height, width and length) was quantified using ImageJ.

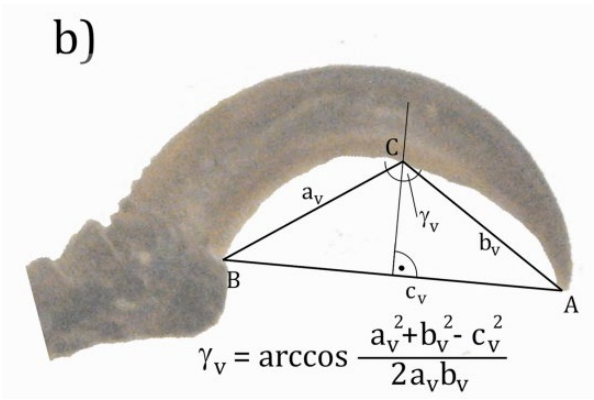

Figure 5: Showing figure 2b in Tinius & Russell (2016), depicting the method used for measuring claw curvature in this study, which was taken from Zani (2000).

This method was chosen because it was able to be carried out by the software used for analysis.

Data Analysis

Data analysis was separated into two chapters. This was because there were two different types of data analysis being performed in this study, one required statistical analysis of the numeric and categorical data collected (Chapter 1), the other required a Finite Element Analysis to be carried out on representative images of geckos' varying claw morphology.

Chapter 1

Chapter 1 of this project aimed to analyse relationships, if any, between geckos' toepad and claw morphologies, in addition to any relationships between either toepad or claw morphology and body weight, habitat occupation and locomotion (arboreal or ground dwelling). This involved a comprehensive set of statistical analyses, using SPSS, being carried out on subsets of species from the original data set of 240 species. There were only 2 species that were grouped into the fifth toepad type category, Partial Division (Fig. 6); this number was too small for any meaningful analyses to be conducted, so were removed from all analyses. The fourth toepad type category originally contained 2 sub-groups; these were grouped together to create a single Paired Division category. This was done to avoid the small number of species in each subgroup from skewing the results and reducing the reliability of the results. Before any parametric statistical test was conducted the data was analyses using a Kolmogorov-Smirnov Test for normality, to see if the data were normally distributed. All the data tested were normally distributed. A Bonferroni correction was also conducted (0.05/n, n=13) as multiple tests were being carried out on the same data set which increases the chances of false positives. Therefore, the significance value was lowered from <0.05 to <0.004, to compensate for this.

For the 152 species that had both "General Habitat" and "Toepad Type" data a chi square test was conducted to find any association between the two groups. Next a series of One-Way ANOVA's were run on the following data, followed by a Post Hoc Tukey test: Body Weight against species categorised via Toepad Type (151 species). A box plot was then created to) to better depict the weight range of the species in each toepad category (Basal, Leaf-Like, Non-Adhesive, Paired Division and Fanned. Body Weight against species categorised via General Habitat (236 species), Body Weight against species categorised either as Arboreal or Ground Dwelling (151 species) (Appendix 2), Claw Length against species categorised via Toepad Type (56 species), Claw Height against species categorised via Toepad Type (56 species), Claw Width against species categorised via Toepad Type (56 species), Claw Curvature against species categorised via Toepad Type (49 species).

Following this a chi square test was run for the 146 species that had both "Toepad Type" and "Claw Presence/Absence" data to find any association between the two groups. Then, a series of linear regressions were ran on the following data: Body Weight against Toepad Width (139 species), Body Weight against Toepad Gap-Width (61 species), Body Weight against Lamellae Number (83 species), Body Weight against Claw Length (56 species), Body Weight against Claw Width (56 species), Body Weight against Claw Height (56 species), Body Weight against Claw Curvature (49 species). These morphological characteristics were size corrected before analysis, by log transforming the variable data and the corresponding body weight data, Log10. If the result was above an r^2 value of 0.3 (Henseler *et al.,* 2009) then they were accepted as a significant relationship. Body Weight against Lamellae was not size corrected as there was no prior expectation for lamellae number to correlate with weight. Plus, no significant relationship was found between claw curvature and body weight, $r^2= 0.012$ (Appendix 2).

In addition to this a phylogenetic tree was created to show the relatedness of each genus of gecko, and to see if there were any preliminary, visual patterns in the evolution of the various toepad types

(Basal, Leaf-Like, Non-Adhesive, Paired Division and Fanned) (Fig. 17). Once again, the fifth toepad group, Partial Division, was not applied due to its small sample size. The tree was created using timetree.org, then the genus' were colour coded based on which of the five toepad type categories (Basal, Leaf-Like, Non-Adhesive, Paired Division and Fanned) the species in this genus possessed, from the species in this research's dataset. It was assumed that all species in each genus would share the same toepads type(s), therefore, species unsampled from each genus, are assumed to have the same toepad types as the species sampled in this research.

Chapter 2

For the second chapter of this project, a Finite Element Analysis (FEA) was carried out on 5 representative species for each toepad type (Basal, Leaf-Like, Non-Adhesive, Paired Division and Fanned). Finite element analyses are ran to discover the comparatively strongest and weakest areas of an object. As species with Partial Division had been removed from the analysis undertaken in Chapter 1, they were also removed from this analysis, for consistency. The representative species also varied in habitat type and claw curvature, to give a greater chance of pattern variation shown in the 2D contour maps. It is likely that the images used do not accurately portray the claw shape as the angle in which the image was taken, may have foreshortened and overestimated the curvature of the claws as they were not placed fully perpendicular to the camera.

The representative species and their toepad and habitat type and claw curvature are as follows:

Hoplodactylus duvacelii – Toepad Type: Basal, Habitat Type: Multi, Microhabitat Type: Rocks and Trees, Claw Curvature: 132°

Pyllodactylus lanei – Toepad Type: Leaf-Like, Habitat Type: Multi, Microhabitat Type: Scrubland and Outcrops, Claw Curvature: 140°

Salutarius cornutus – Toepad Type: Non-Adhesive, Habitat Type: Tree, Microhabitat Type: Tropical Forest, Claw Curvature: 112°

Lygodactylus chobiensis – Toepad Type: Paired Division, Habitat Type: Tree, Microhabitat Type: Forest debris/floor, Claw Curvature: 107°

Ptyodactylus guttatus – Toepad Type: Fanned, Habitat Type: Saxicolous, Microhabitat Type: Semi desert, Claw Curvature: 93°

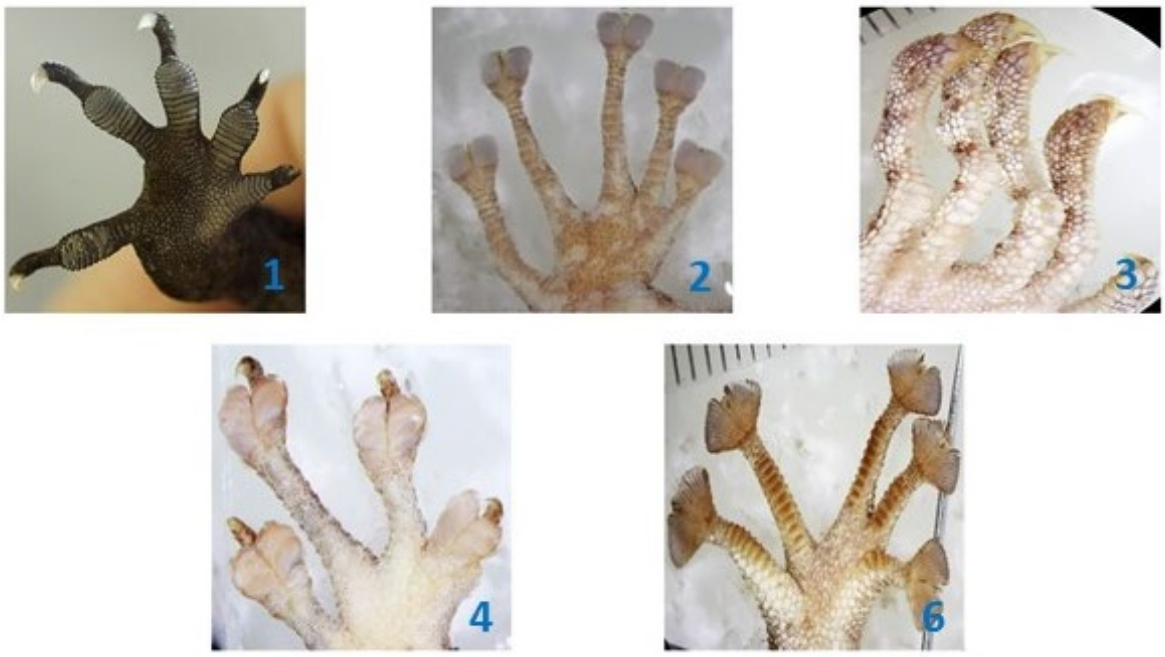

Figure 6: The original images for each species chosen as a representative species with claws, for each toepad type. Top Row: *Hoplodactylus duvacelii*, *Phyllodactylus lanei*, *Salutarius cornutus*. Bottom Row: *Lygodactylus chobiensis*, *Ptyodactylus guttatus*.

To begin, the claw image was imported into an image editing software called Inkscape, where the outline of each claw was traced and filled. The file type (.eps) was then converted (to .svg) using a website named Convertio (Convertio, 2021), before being imported into another software named Blender which converted the file type for a final time (to .stl), so it was able to be processed in a multi-paradigm programming language and numeric computing software called MATLAB. The contour maps were then created using an FEA Multiphysics tool.

A two-dimensional plane stress analysis was carried out on each claw tracing. The plane stress analysis assumes that the object in question is loaded in a single flat plane. The force exhibited on each claw was determined by converting the body weight of the individual representative of the species, from grams to Newtons. The Youngs Modulus assigned was 2.7GPa (Gigapascals) as this is a standard measure of the stiffness of keratin in claws (Wang *et al.,* 2016) and the Poisson ratio for keratin was 0.3 (Manning *et al*., 2009). After following steps 11-23 of an FEATool Multiphysics Tutorial (FEATool Multiphysics) the contour maps were created. The forces were applied perpendicular, at the tip of each claw to depict how the claw would interact, naturally, when in use by the gecko. The base of each claw (i.e., where directly attached to the digit) were held constant, as this depicts how that area would deal with external forces when in use.

The purpose of the contour maps was to determine, using the colour coded key, the comparative strongest and weakest point(s) of each claw, when under stress. The weakest points being the area(s) most susceptible to breakage when under excessive force, e.g., when running or climbing. These maps allowed for the comparison, across species, genus, and habitat type, of claw morphology.

Results

Chapter 1: Toepad and Claw Morphology

Across all toepad type groups (Basal, Leaf-Like, Non-Adhesive, Paired Division and Fanned), a total of 146 species, claws have a statistically significantly higher presence than absence count, across toepad types (X= Chi Square Test, 4 df, p= 0.002) (Fig. 7). Absence of claws in one species with "Non-Adhesive" toepads is an unexpected finding as that group is ground dwelling. Meaning one species, in this study, *Chondrodactylus angulifer*, is lacking both claws and adhesive toepads. Statistically significant findings were seen between toepad type and claw length, width and height (Length: F= 5.334, One-Way ANOVA, 4df, p= 0.001. Width: F=8.105, One-Way ANOVA, 4 df, p= 0.000. Height: F= 4.537, One-Way ANOVA, 4df, p= 0.003). The mean representative values for claw length and width for 56 species of gecko show that those with Leaf-Like toepads, overall, have the smallest claw size (Fig. 8) but also are the lighter species (Fig. 10). However, all toepad types follow the trend of claw length being the largest measurement, then height followed by width, aside from the Fanned category, where the claw height is the largest measurement, then length, then width (Fig. 8).

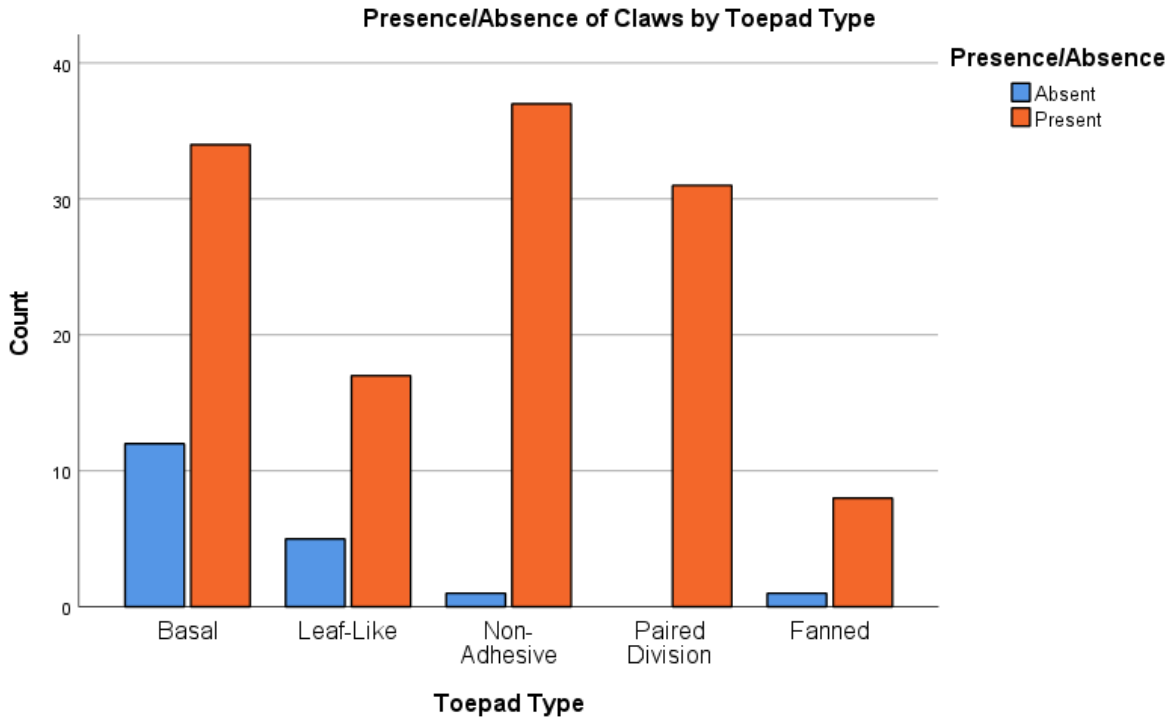

Figure 7: Presence and absence of claws in 146 species of gecko, grouped via toepad type (Basal, Leaf-Like, Non-Adhesive, Paired Division and Fanned). Refer to Fig.2 for toepad type reference images. A chi-square test showed that claws were statistically significantly more likely to be absent in gecko species with Basal and Leaf-Like toepads in comparison to those with Non-Adhesive, Paired Division and Fanned toepads (X= Chi Square Test, 4 df, p= 0.002).

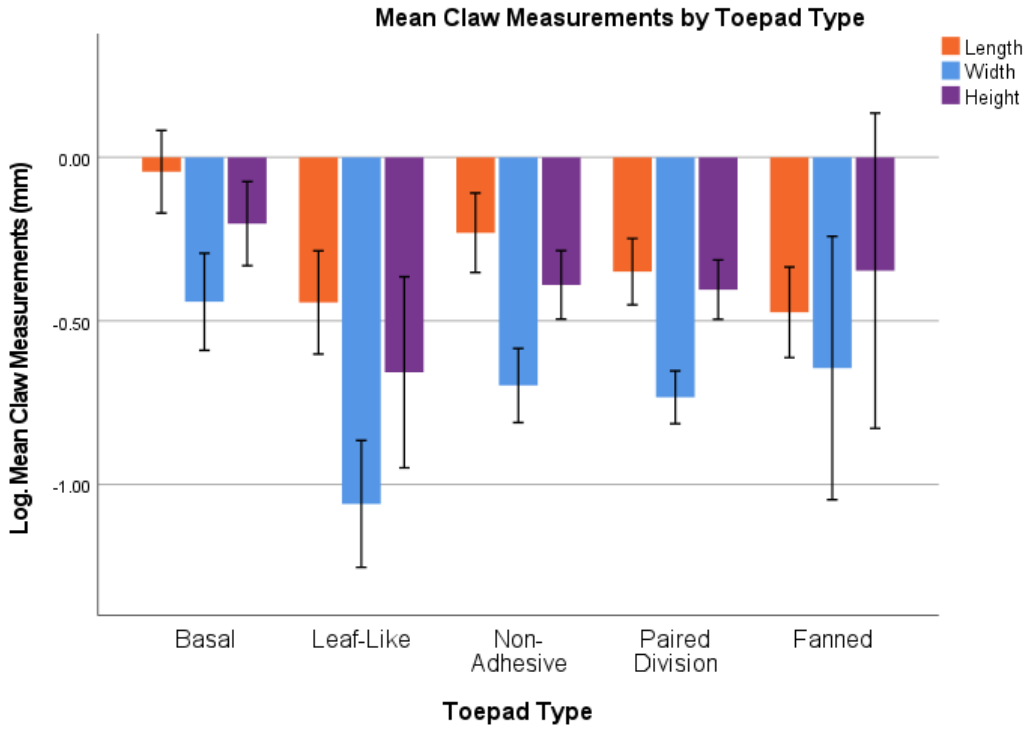

Figure 8: Mean values for the logarithmically transformed claw height, length and width of 56 species of gecko, grouped via toepad type (Basal, Leaf-Like, Non-Adhesive, Paired Division and Fanned). Refer to Fig.2 for toepad type reference images. Length: F= 5.334, One-Way ANOVA, 4df, p= 0.001. Width: F=8.105, One-Way ANOVA, 4 df, p= 0.000. Height: F= 4.537, One-Way ANOVA, 4df, p= 0.003. Post Hoc Tuket test found significant differences between Basal and Leaf-Like claw length, width and height, p= 0.009, p= 0.000, p= 0.003, respectively. In addition to significance between Basal and Paired Division claw length, p= 0.005. Error bars at the 95% confidence level.

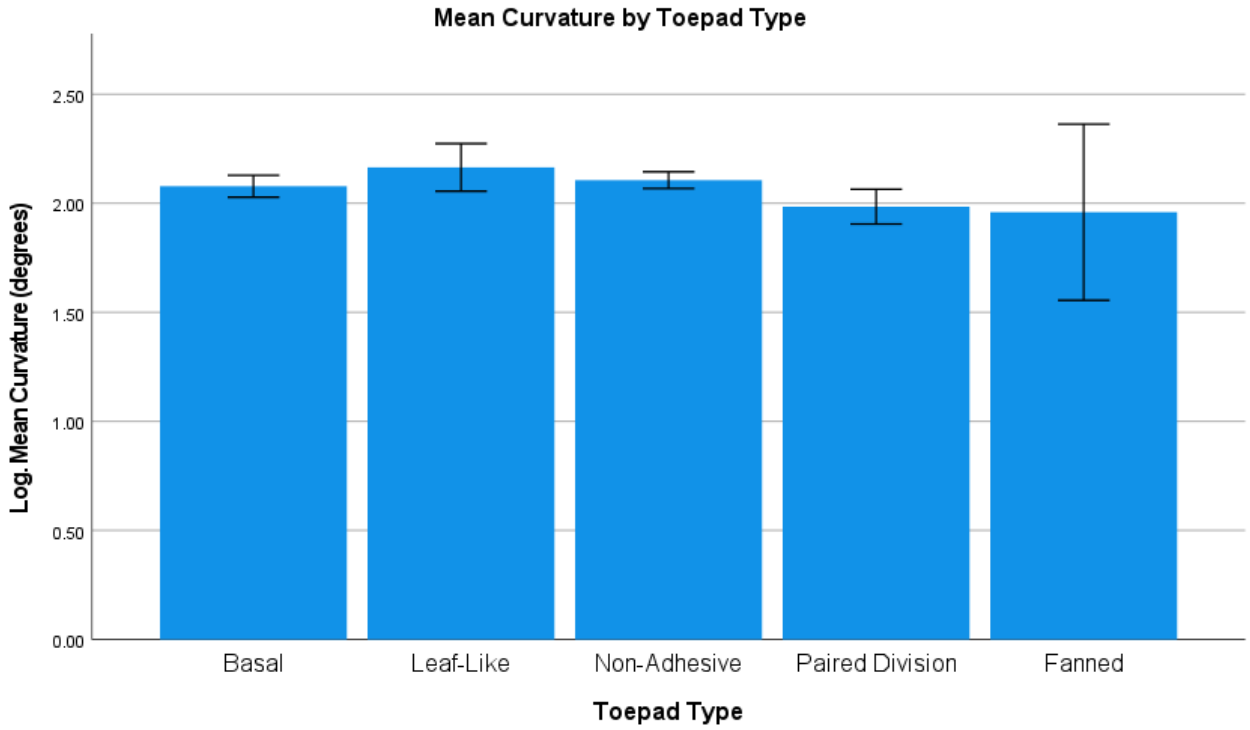

Figure 9: Mean representative values for claw curvature of 49 species of gecko, grouped via toepad type (Basal, Leaf-Like, Non-Adhesive, Paired Division and Fanned). Refer to Fig.2 for toepad type reference images. Statistical significance was found in the logarithmically transformed mean claw curvature between toepad types, ($F= 4.706$, One-Way ANOVA, 4 df, $p= 0.003$). Post Hoc Tukey Test found no statistically significant differences between the groups. Error bars at the 95% confidence level.

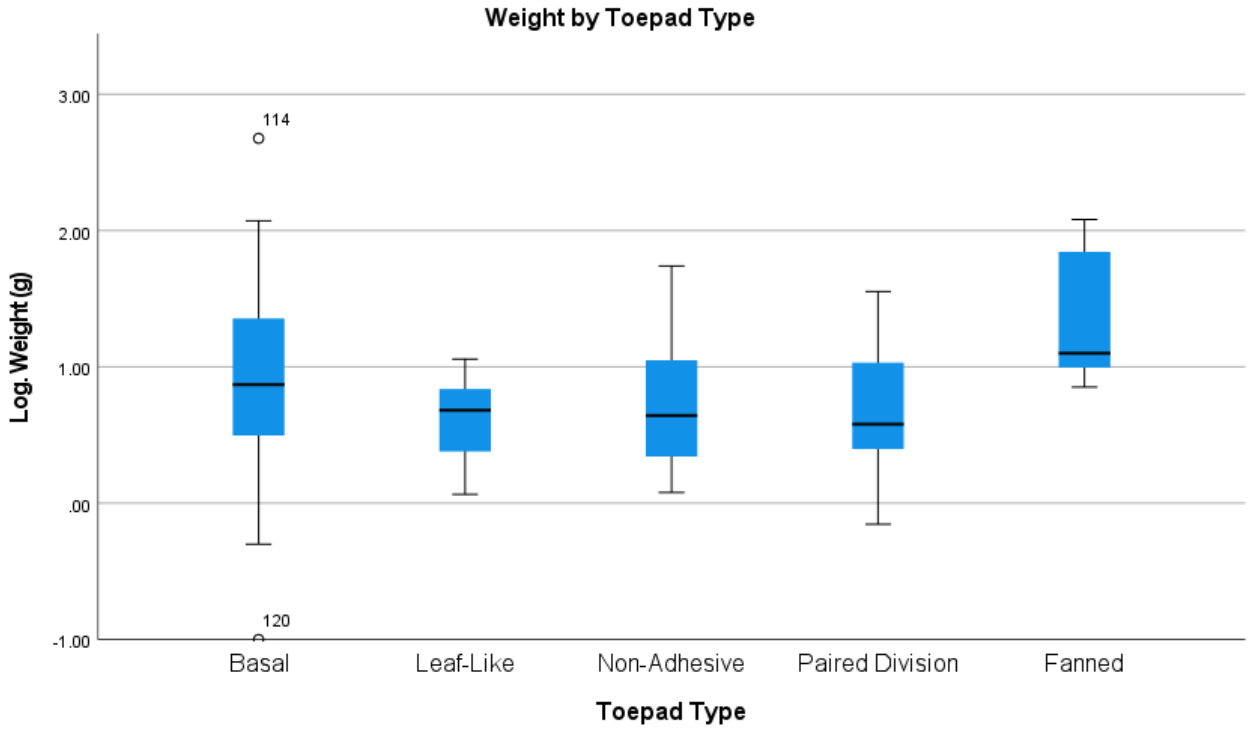

Figure 10: Box plot depicting the weight ranges of the gecko species (n=148) in each toepad type (Basal, Leaf-Like, Non-Adhesive, Paired Division and Fanned) group. Refer to Fig.2 for toepad type reference images. ° Represents the outlying data points. A One-Way ANOVA showed statistically significant differences between the logarithmically transformed weight of the species in each toepad type (F= 4.608, One-Way ANOVA, df= 4, p= 0.002). Those in the Fanned toepad category were, on average, the heaviest species. Post Hoc Tukey Test found statistically significant relationships between Fanned and Leaf-Like and Paired Division (p= 0.002, p= 0.004 respectively). Error bars at the 95% confidence level.

The results for mean claw curvature and toepad type showed statistical significance (n=49. F= 4.706, One-Way ANOVA, 4 df, p= 0.003): between claw curvature and toepad type for the species in this study. The gecko species grouped in the Leaf-Like category have the straightest claws, overall (Fig. 9). This goes against the expected result of the ground dwelling geckos (Non-Adhesive) having the straightest claws, as many of these species only climb as efficiently as what their claws allow them to; as they cannot also rely on their toepads due to their lack of an adhesive system. The results for the arboreal gecko species in Basal, Paired Division and Fanned follow the expected results of having claws with more of a curvature than the ground dwelling species. The species in Paired Division are arboreal, and typically have the most curved claws (Fig. 9). The boxplot of mean weight of 148 species of gecko (Fig. 10) confirms that Fanned contains the heaviest geckos (F= One-Way ANOVA, 4 df, p= 0.002), with an upper range of weight 2x that of the group with the lightest lower range, Leaf-Like. Having an arboreal group be the heaviest in weight, goes against the assumption that the ground dwelling gecko species (Non-Adhesive) would be the heavier species. Strong relationships were found between the logarithmically transformed and therefore size corrected data for claw length and body weight (n=56. r^2= 0.329) (Fig. 14), width and body weight (n=56. r^2= 0.361) (Fig. 16), height and body weight (n=56. r^2= 0.416) (Fig. 17), toepad width and body weight (n=139. r^2= 0.449) (Fig. 11), toepad gap-width and body weight (n=61. r^2= 0.395) (Fig. 12) and lamellae number and body weight (n=83. r^2= 0.361) (Fig. 13).

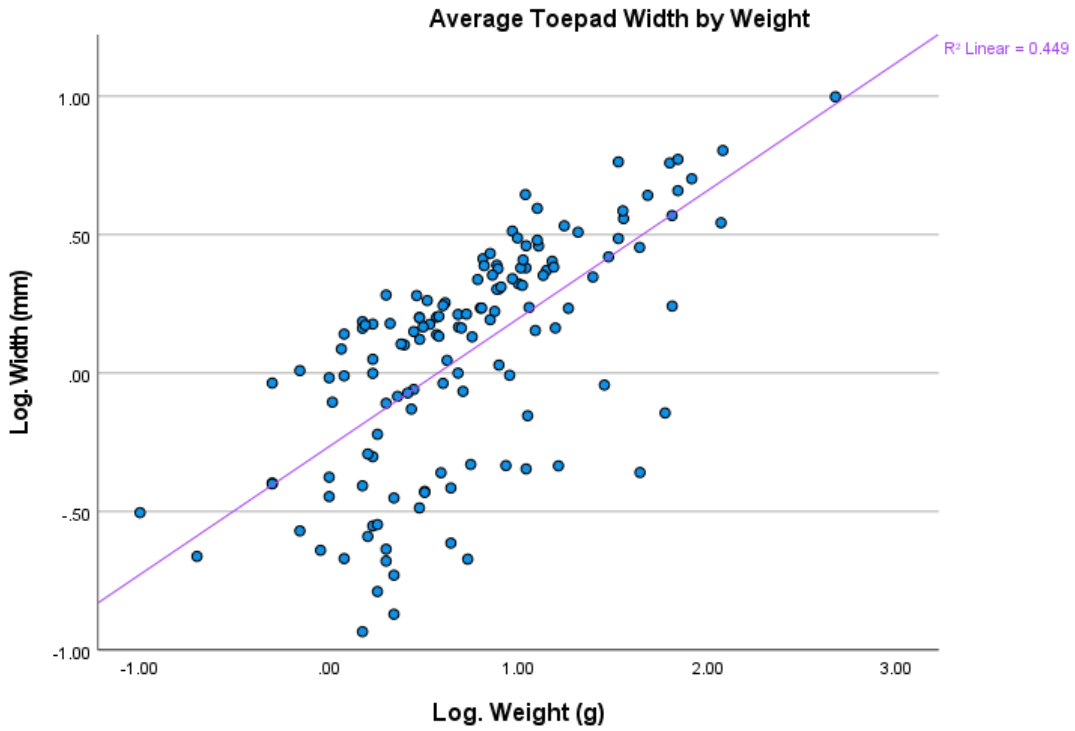

Figure 11: Linear regression of the logarithmically size corrected toepad width and weight values for 139 species of gecko, showing that there is a strong relationship between toepad width and body weight (r^2= 0.449), among these species of gecko.

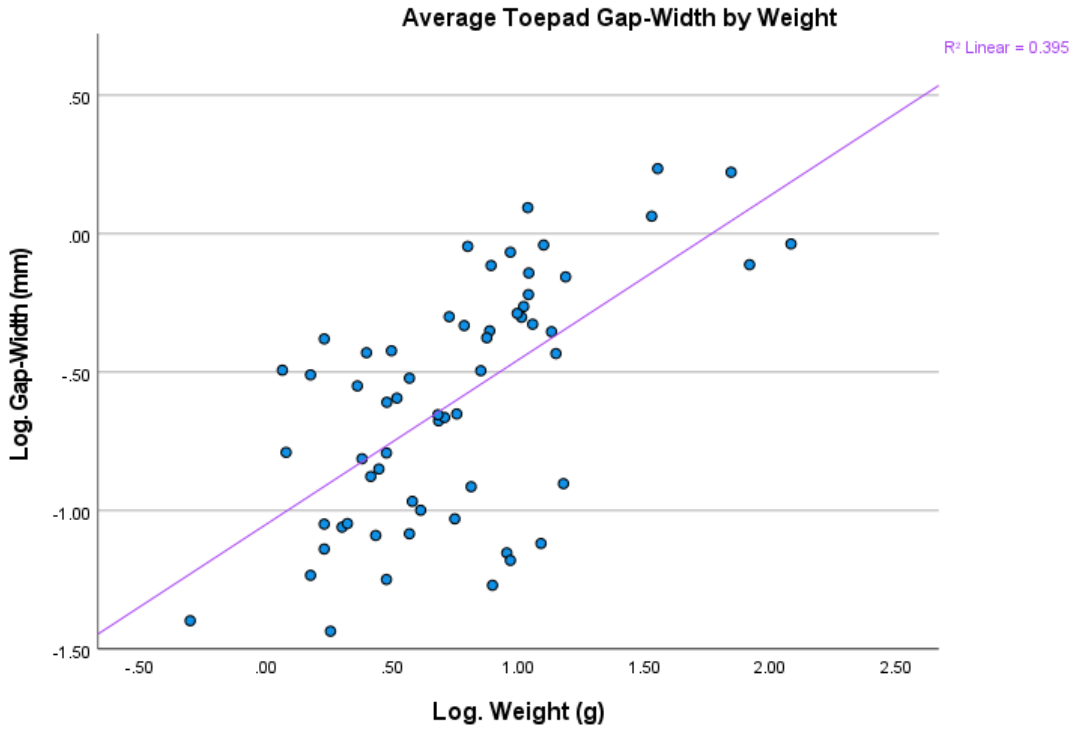

Figure 12: Linear regression of the logarithmically size corrected toepad gap-width and weight values for 61 species of gecko, showing that there is a strong relationship between toepad gap-width and body weight (r^2= 0.395), among these species of gecko.

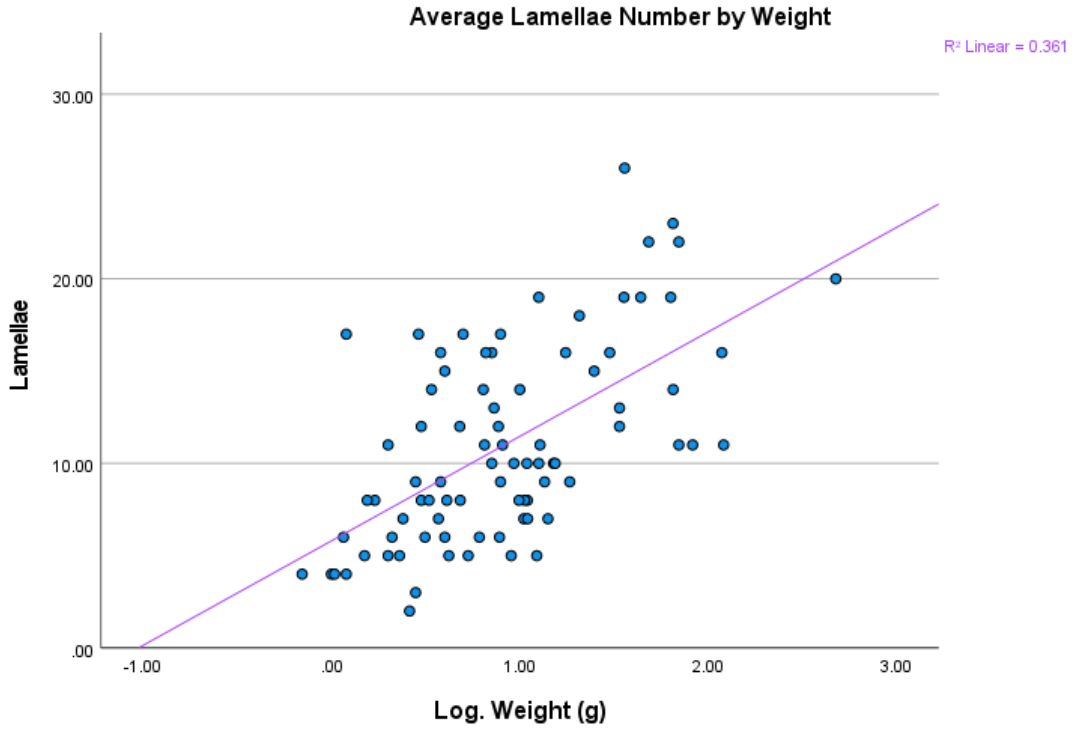

Figure 13: Linear regression of the logarithmically size corrected weight values against lamellae number for 83 species of gecko, showing that there is a strong relationship between lamellae and body weight (r^2= 0.361), among these species of gecko.

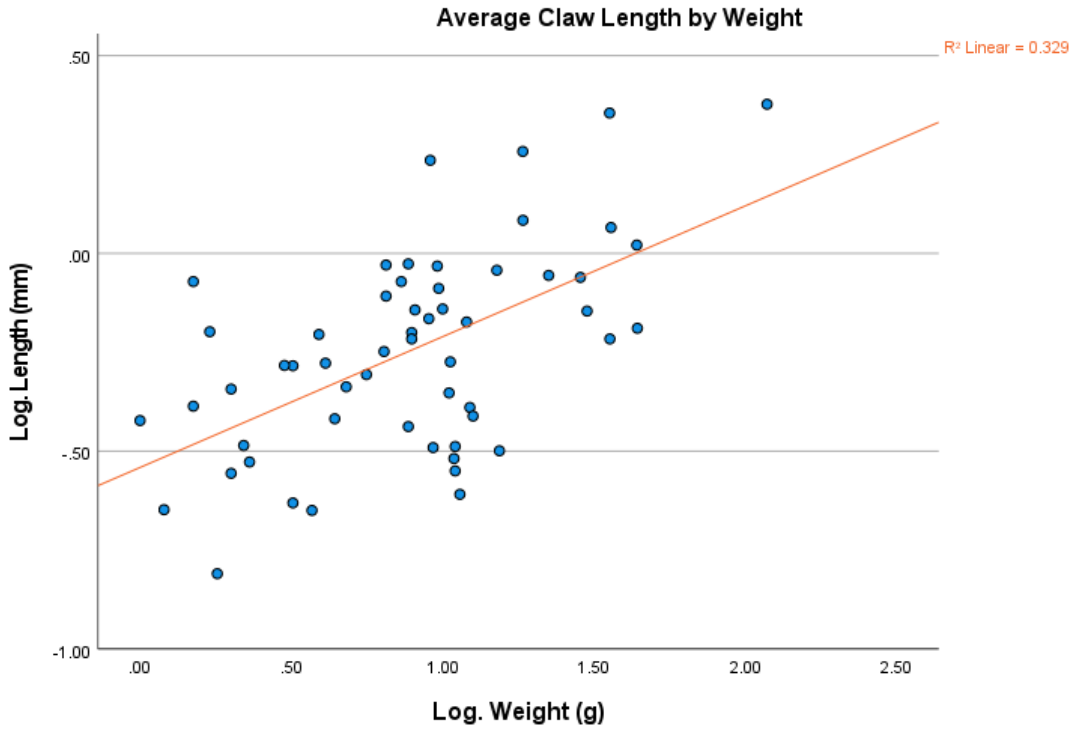

Figure 14: Linear regression of the logarithmically size corrected claw length and weight values for 56 species of gecko, showing that there is a strong relationship between claw length and body weight (r^2= 0.329), among these species of gecko.

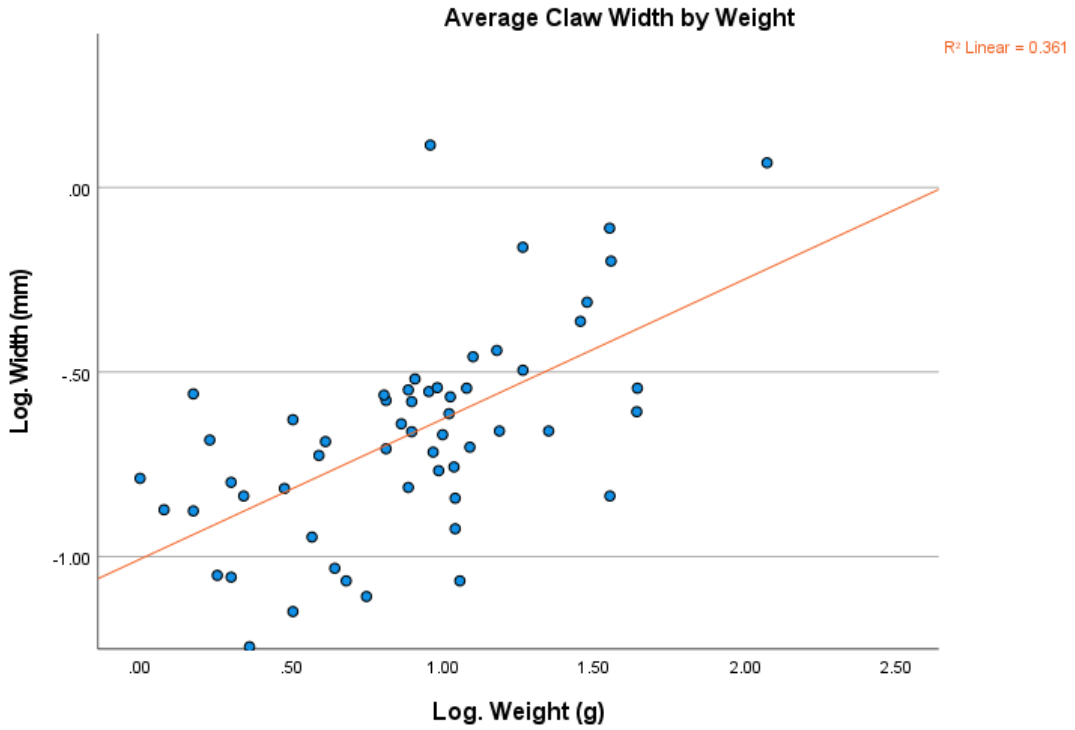

Figure 15: Linear regression of the logarithmically size corrected claw width and weight values for 56 species of gecko, showing that there is a strong relationship between claw width and body weight (r^2= 0.361), among these species of gecko.

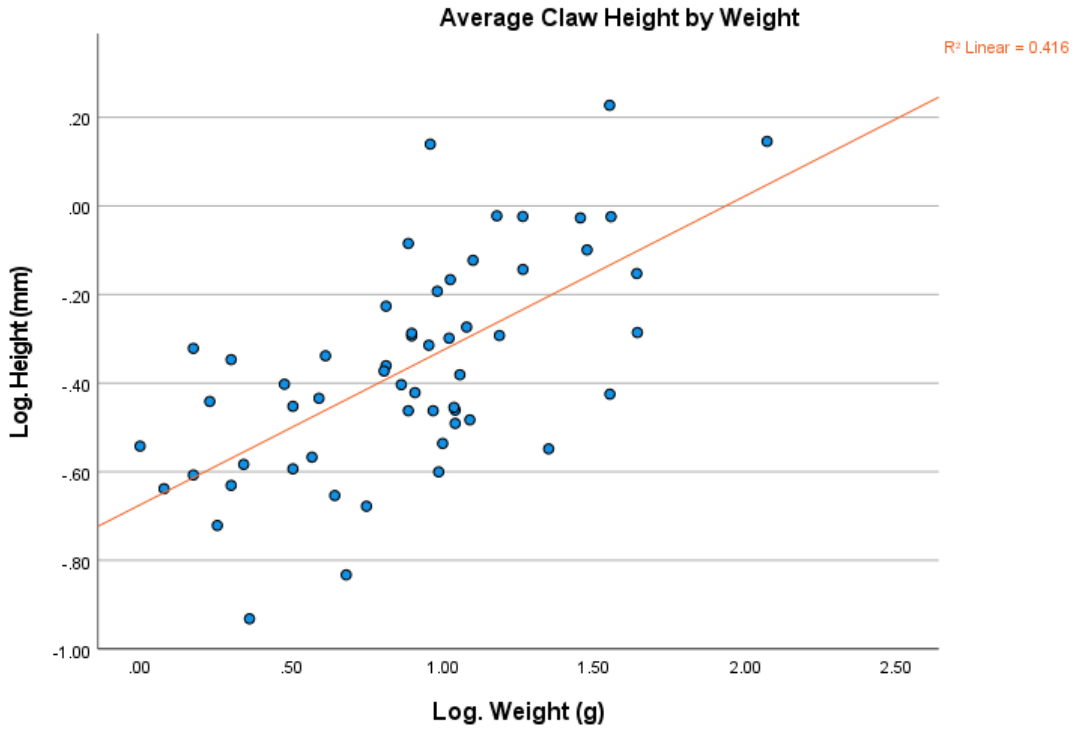

Figure 16: Linear regression of the logarithmically size corrected claw height and weight values for 56 species of gecko, showing that there is a strong relationship between claw height and body weight (r^2= 0.416), among these species of gecko.

Statistical significance was not found when comparing the logarithmically transformed mean weight of the gecko species in each habitat type (F= One-Way ANOVA, 3 df, p= 0.088. Ground, n=51. Multi, n=49. Saxicolous, n=41. Tree, n=95.). Geckos categorised as having multiple general habitat types – "Multi", have a medium average weight in comparison to the geckos in the Tree (heaviest) and Ground (lightest) general habitat groups (Fig. 17). The findings of the chi square test for association between toepad type and general habitat occupation were statistically significant (n=148. X= Chi Square Test, 12 df, p= 0.002.) Geckos with Fanned toepads appear in the least amount of different 'General Habitat' types, in comparison to the species with Basal, Leaf-Like, Non-Adhesive and Paired Division, which appear in all the different 'General Habitat' categories (Fig. 18).

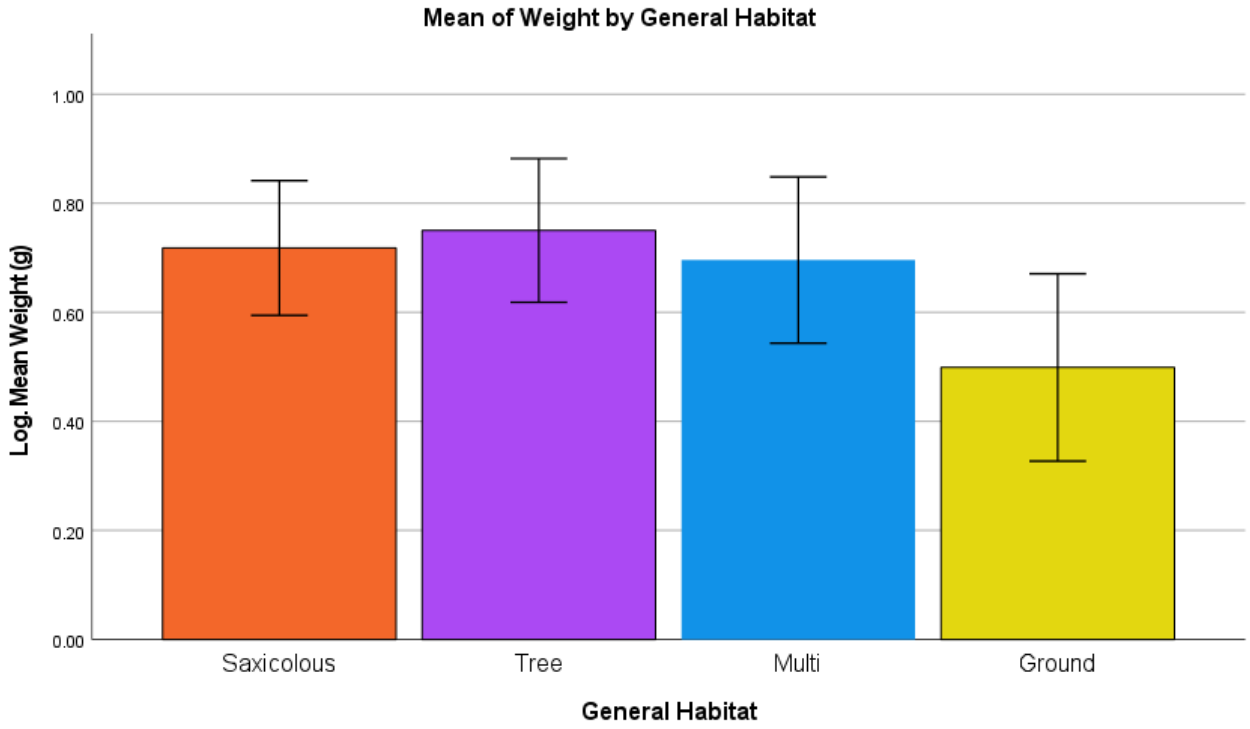

Figure 17: The mean logarithmically transformed weight of geckos (n=236) that live in each General Habitat type. The findings of this statistical analysis showed no significance between the mean weights of the gecko species found in each general habitat type (F= 2.204, One-Way ANOVA, 3 df, p= 0.088). Ground, n=51. Multi, n=49. Saxicolous, n=41. Tree, n=95. Error bars at the 95% confidence level.

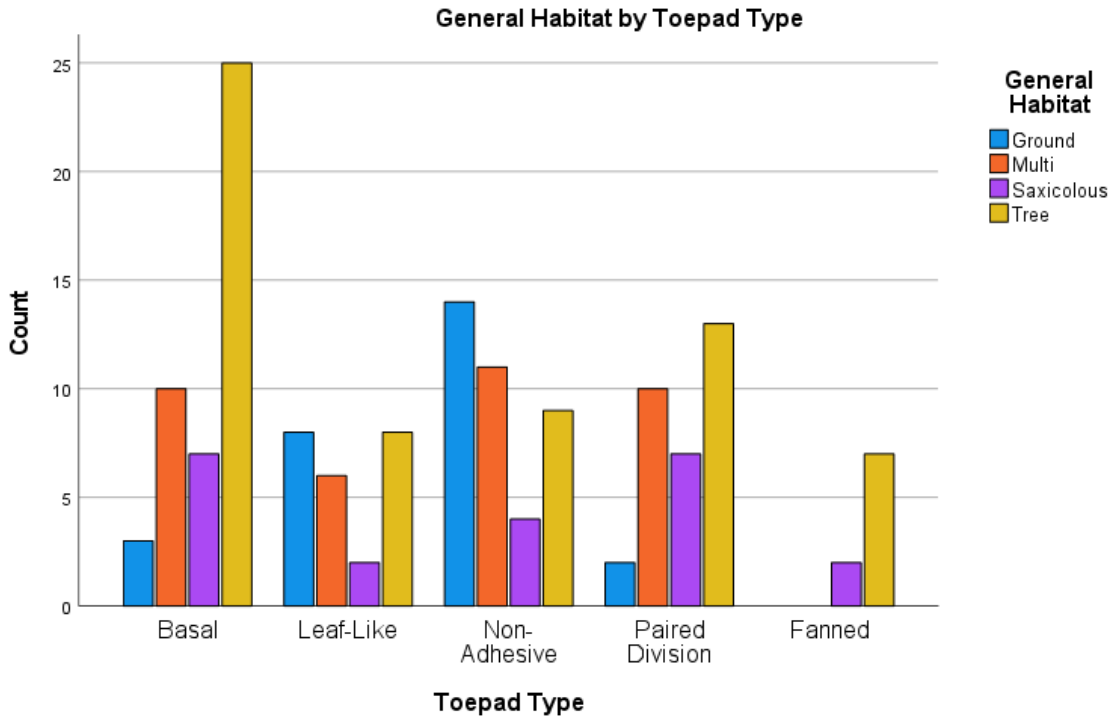

Figure 18: Count of the amount of gecko species (n=148) with each toepad type (Basal, Leaf-Like, Non-Adhesive. Paired Division and Fanned)), found in each general habitat type. Statistical significance was found between these groups (X= Chi Square Test, 12 df, $p < 0.002$), showing association between gecko toepad type and their general habitat. *7 cells had an expected count of less than 5.

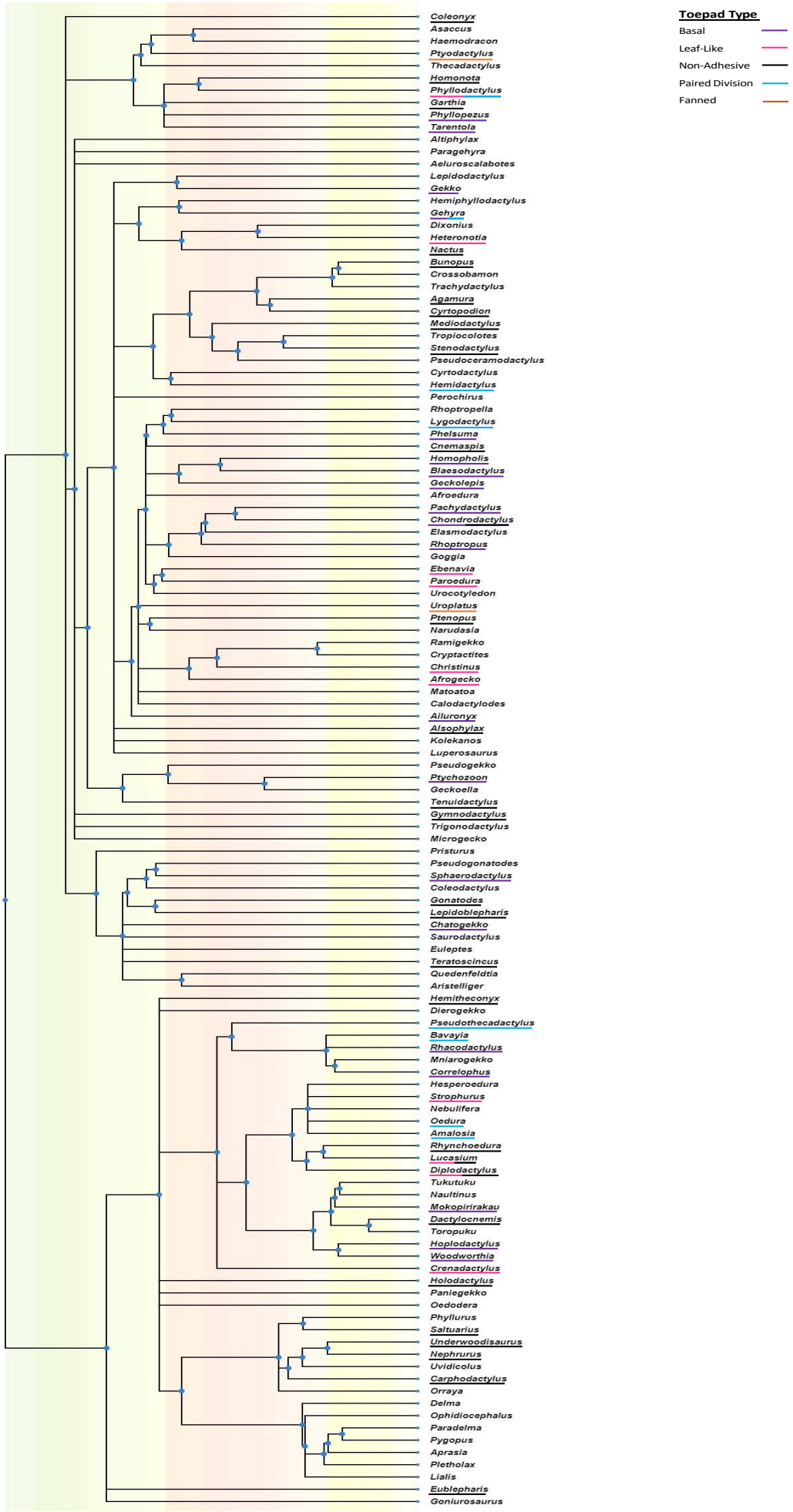
Toepad Type
Basal
Leaf-Like
Non-Adhesive
Paired Division
Fanned
Coleonyx
Asaccus
Haemodracon
Ptyodactylus
Thecadactylus
Homonota
Phyllodactylus
Garthia
Phyllopezus
Tarentola
Altiphylax
Paragehyra
Aeluroscalabotes
Lepidodactylus
Gekko
Hemiphyllodactylus
Gehyra
Dixonius
Heteronotia
Nactus
Bunopus
Crossobamon
Trachydactylus
Agamura
Cyrtopodion
Mediodactylus
Tropiocolotes
Stenodactylus
Pseudoceramodactylus
Cyrtodactylus
Hemidactylus
Perochirus
Rhoptropella
Lygodactylus
Phelsuma
Cnemaspis
Homopholis
Blaesodactylus
Geckolepis
Afroedura
Pachydactylus
Chondrodactylus
Elasmodactylus
Rhoptropus
Goggia
Ebenavia
Paroedura
Urocotyledon
Uroplatus
Ptenopus
Narudasia
Ramigekko
Cryptactites
Christinus
Afrogecko
Matoatoa
Calodactylodes
Ailuronyx
Alsophylax
Kolekanos
Luperosaurus
Pseudogekko
Ptychozoon
Geckoella
Tenuidactylus
Gymnodactylus
Trigonodactylus
Microgecko
Pristurus
Pseudogonatodes
Sphaerodactylus
Coleodactylus
Gonatodes
Lepidoblepharis
Chatogekko
Saurodactylus
Euleptes
Teratoscincus
Quedenfeldtia
Aristelliger
Hemitheconyx
Dierogekko
Pseudothecadactylus
Bavayia
Rhacodactylus
Mniarogekko
Correlophus
Hesperoedura
Strophurus
Nebulifera
Oedura
Amalosia
Rhynchoedura
Lucasium
Diplodactylus
Tukutuku
Naultinus
Mokopirirakau
Dactylocnemis
Toropuku
Hoplodactylus
Woodworthia
Crenadactylus
Holodactylus
Paniegekko
Oedodera
Phyllurus
Saltuarius
Underwoodisaurus
Nephrurus
Uvidicolus
Carphodactylus
Orraya
Delma
Ophidiocephalus
Paradelma
Pygopus
Aprasia
Pletholax
Lialis
Eublepharis
Goniurosaurus

Figure 19: A phylogenetic tree (timetree.org) showing the relatedness of all genus' within the Gekkota group. The genus' in which toepad type data was collected, for this research, have been underlined and colour coded, each colour representing a different toepad type, as is shown in the key above. Some genus' have varying toepad types across species, in these cases, they were underlined with the colours that represented all of the toepad types that the species' in that genus, in this data set, have.

Non-Significant, Preliminary Results

The Chi Square Test carried out for association between the 'Toepad Types 1, 2, 3, 4 and 6' against 'Microhabitat' (Species, n=148) produced unreliable results as the data did not meet the test assumptions (X= Chi Square Test, 96 df, p= 0.020). Refer to Fig.2 for toepad type reference images. However, there were a couple of interesting preliminary patterns, as the habitats that geckos with 'Toepad Type 2 and 6' aren't as varied as 'Toepad Types 1, 3 and 4', with 'Toepad Type 1' being the most varied category (Fig. 17).

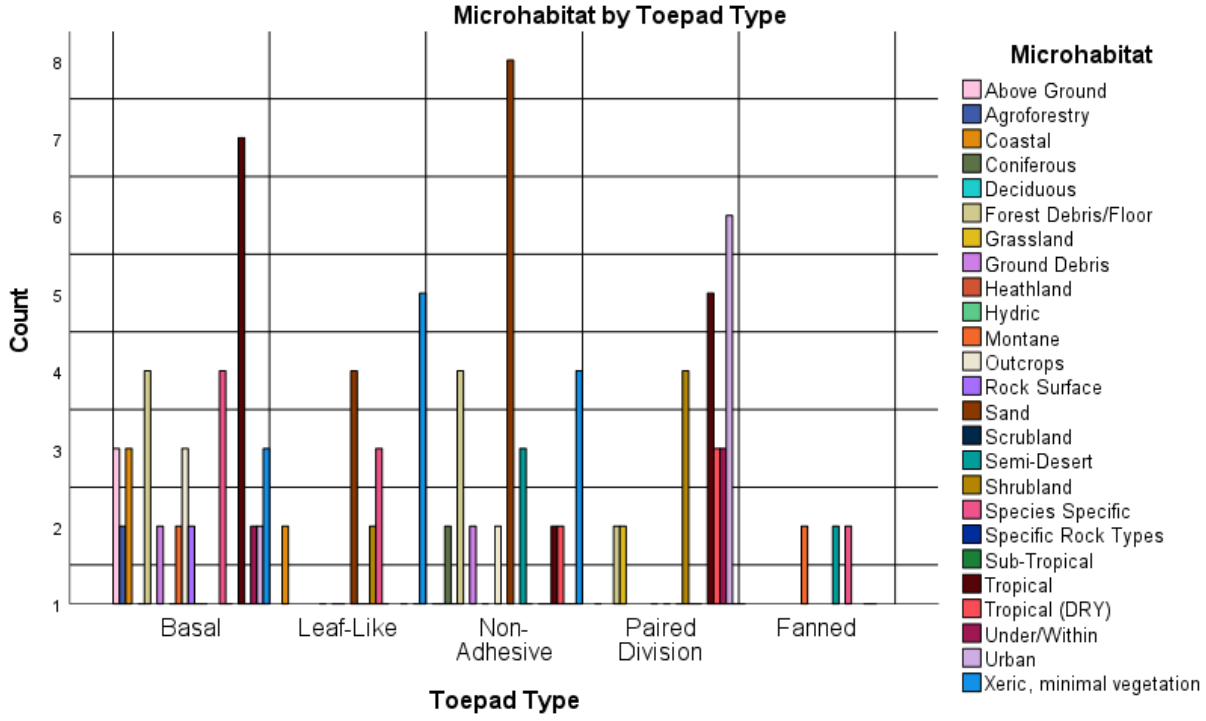

Figure 20: Count of the number of species (n=148) of gecko with each toepad type (1, 2, 3, 4 and 6) found in each microhabitat type (X= Chi Square Test, 6 df, p= 0.020). The statistical significance found between gecko toepad type and their microhabitat should be treated with caution, as 125 cells had an expected value of less than 5. Therefore, the data did not meet the assumptions of the test. However, it does show interesting preliminary patterns, regarding the habitats that geckos with toepad types 2 and 6 are found. As these aren't as varied as the other three toepad types, with toepad type 1 being the most varied.

Other non-significant results can be found in Appendix 2.

Chapter 2: Finite Element Analysis of Claws

Finite Element Analyses were conducted on five representative species of gecko, one for each toepad type, whilst also making sure that the claws were from species that occupied different habitat types (general and micro) also. The representative species for Basal and Leaf-Like (Fig. 22) follow the same pattern regarding the points of their claws most susceptible to stress. They seemingly have the strongest claws, in that they have the smallest areas susceptible to stress and therefore breakage. They also have similar curvatures (132°, 140° respectively) and are categorised in the "Multi" general habitat grouping. The representative species for Non-Adhesive (ground dwelling geckos) is the claw that seems to be the most susceptible to breakage, with the largest areas, comparatively, that are vulnerable to stress. The representative species for Paired Division and Fanned are similar in that they are the most curved claws (107° and 93° respectively). However, they differ in both their general and micro habitat types, with the representative of Paired Division living among vegetation and that of Fanned in rocky environments. The representative claw for Paired Division is more susceptible to stress and breakage and less curved, than the representative claw for Fanned.

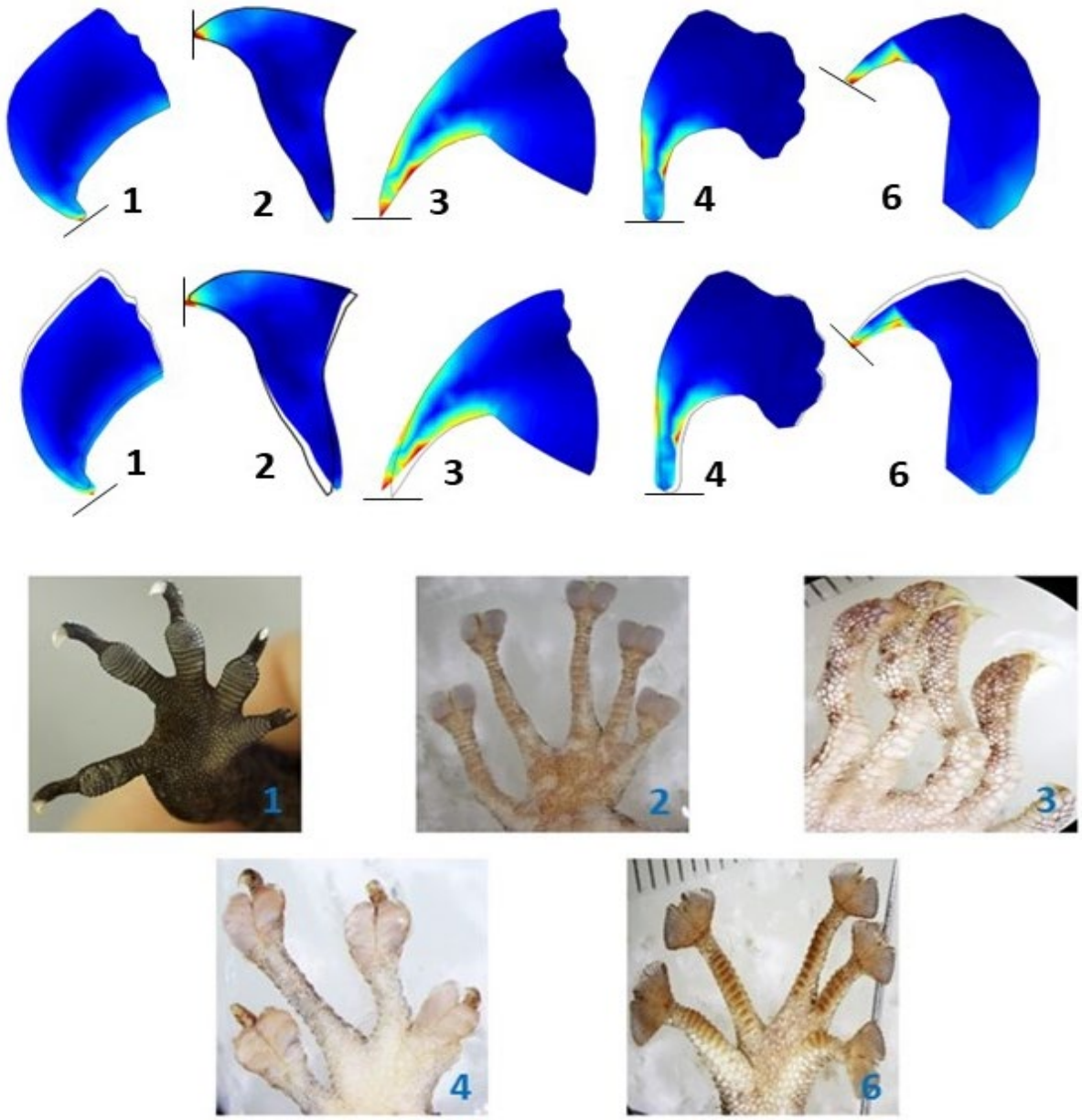

Figure 21: 2-dimensional stress contour maps created using Finite Element Analysis on the claw of the fourth toe of either the left or right hind foot (for continuity) of 5 different gecko species. The forces were applied perpendicular to and at the tip of each claw, to represent how the claw would interact naturally with the substrate. Each species was from a different toepad type category, along with varying habitat types and curvature. 1. ***Hoplodactylus duvacelii*** – Toepad Type: Basal, General Habitat: Multi, Microhabitat: Rocks and Trees, Claw Curvature: 132°. 2. ***Phyllodactylus lanei*** – Toepad Type: Leaf-Like, General Habitat: Multi, Microhabitat: Scrubland and Outcrops, Claw Curvature: 140°. 3. ***Salutarius cornutus*** – Toepad Type: Non-Adhesive, General Habitat: Tree, Microhabitat: Tropical Forest, Claw Curvature: 112°. 4. ***Lygodactylus chobiensis*** – Toepad Type: Paired Division, General Habitat: Tree, Microhabitat: Forest Debris/Floor, Claw Curvature: 107°. 6. ***Ptyodactylus guttatus*** – Toepad Type: Fanned, General Habitat: Saxicolous, Microhabitat: Semi Desert, Claw Curvature: 93°. Top row: the claws in a stationary position, the line representing how each claw would come into contact with a surface. Bottom row: the deformation plot of the same claws, depicting their possible movement when in use, the line representing how each claw would come into contact with a surface.

Discussion

This study's analyses have shown that there are statistically significant relationships between gecko claw morphology and toepad type, as well as their claw presence/absence and their toepad type. There are also statistically significant relationships between gecko body weight and their toepad type, as well as their general habitat occupation and their toepad type. This section will critically evaluate the findings and patterns seen in the results for both chapter one and two. Before considering, in more detail, the links, if any, to the current literature findings. Then, the implications of these results on the current literature, in addition to the direction(s) that should be taken by any future studies.

Chapter 1:

The aim of this chapter was to discover relationships, if any, between geckos' toepad morphology and their habitat occupation. Plus, their toepad morphology and claw morphology and/or claw presence/absence. In addition to finding relationships, if any, between body weight and toepad morphology. The following hypotheses were tested to achieve these aims:

Arboreal geckos with leaf-like adhesive toepads will occupy a wider range of microhabitats than those with basal adhesive toepads. In the example given by Russell and Delaugerre (2016) of two gecko species observed on Giraglia Island, geckos with different toepad types occupied different habitat(s). The species with leaf-like toepads was observed occupying more habitat types than the basally padded gecko, which was only seen using one.

Body weight will factor in determining the geckos' capacity for arboreality, due to the upper size limits on equal load sharing across the adhesive toepad as well as the morphological size constraints on increasing the adhesive toepad size (Russell and Johnson 2014: Labonte *et al.* 2016: Labonte and Federle, 2015). *Therefore, geckos that are ground dwelling will, typically, be heavier than those that are arboreal.*

An increase in claw curvature will be seen in geckos with an arboreal locomotive capacity, compared to those that are ground dwelling as these are known to have straighter claw shapes. This would fit with Birn-Jeffery *et al*. (2012)'s discoveries in their study on extant bird and lizard pedal claws.

Geckos that are arboreal will have a reduced claw size compared to those that are ground dwelling, as they can also rely on their adhesive toepads for climbing. As discussed by Russell and Gamble (2019), as pad-bearing geckos can lift their claws to procure a better purchase on the inclined substrate whilst using their adhesive toepads to uphold their grip.

Phylogenetic Relatedness:

Phylogeny must be considered when conducting biological research between and/or across taxa. The purpose of phylogeny is to depict and organise the evolutionary history of organisms to help better understand their relatedness to one another, over evolutionary time. Not only does this practice help researchers to better understand and account for the vast amount of evidence that supports the theory of evolution, but it also helps provide answers to potential questions their research projects have discovered, when considering how traits/organisms have evolved (Baum, 2008). This is especially true when researching changes in morphology over evolutionary time, like this project does. Phylogeny was considered in this project in the form of a phylogenetic tree. This tree illustrated the relatedness of the Gekkota order, at the genus level (Fig. 19). Whilst also being modified to show what toepad morphological category the species, researched in this project, possess. This was done to help visualise any trends/patterns in the evolution of their toepad morphology. In addition to, seeing if there was/wasn't any close relatedness between toepad types/genus' which would explain any similar results the varying toepad types had. Plus, it could

rule out relatedness as a factor/reason if the toepad and/or claw morphology results are similar between/across toepad types. Because if the genus' of those species aren't related, but show similar morphological results, then it allows for the conclusion that there is another reason behind these similarities/patterns, other than relatedness.

To improve on this, if this project were to be re-done then each regression test would be run alongside a phylogenetic generalised least square (PGLS) correction. PGLS' are a useful comparative method as they produce covariant estimates that show to which extent, via residuals from the least square regression line, the traits tested are similar, based on the phylogenetic relationship(s) between the data being tested (Symonds & Blomberg, 2014). This method of comparative analysis was not conducted on the data collected during this research due to the time constraints of the project. However, if done again or added to in the future, PGLS' would be carried out on all morphological regression data. Doing so would either strengthen the validity of the significance values, by showing that there is a reason other than phylogeny behind the patterns/trends shown when comparing specific morphological traits, across genus'; or that these trends/patterns can be explained due to phylogenetic relatedness. Therefore, more confidence would be able to be inferred on the interpretation of the results and the reasons behind them.

Claw Presence/Absence:

A species was classified as being absent of claws if no claws were present on any of their digits. However, the species where claws were present didn't necessarily possess claws on all their digits. Claw absence is visible in some gecko species across all toepad types, excluding those in the Paired Division category (Fig. 7). The absence of claws in at least one ground dwelling species of gecko (Non-Adhesive) is an unexpected finding as it is assumed that if a gecko lacks adhesive toepads, as ground-dwelling ones do, then they would rely on their claws for climbing (although limited to what can be achieved without an adhesive system) and various other purposes when moving around their environment. Beyond attachment, geckos are also known to use their claws to assist with their foraging behaviour, particularly digging for food, and males also use their claws to hold females in place during mating (Henkel & Schmidt, 1991). However, this result suggests that at least one species of ground dwelling geckos (*Chondrodactylus angulifer*), perhaps more, aren't using either claws or adhesive toepads to help with locomotion or certain other behaviours. Interestingly, *Chondrodactylus angulifer* is categorised as living in a 'Multi' general habitat type. As stated previously by Gamble *et al.,* (2012) the genus *Chondrodactylus* notably lost its adhesive system when they adapted to burrowing in loose sand rather than living in saxicolous environments. Could this claw loss be another functionally adaptive morphological trait to allow this genus to successfully occupy varying habitat types? Further research is needed to better understand the true significance of this claw presence/absence result (which was statistically significant at $p= 0.002$) (Fig. 7), and the reasons for the claw loss observed in some gecko species, particularly in those that are ground dwelling. Phylogeny will also need to be considered in greater detail to determine if there are any other species, from genera outside of *Chondrodactylus* that possess neither adhesive toepads or claws, or is it a unique trait to this genus alone.

Claws are more often present than absent across all the toepad types in this study. Four of the five toepad groups analysed, consist of species with adhesive toepads, Basal, Leaf-Like, Paired Division and Fanned, of varying morphology. Within three of these four groups, Basal, Leaf-Like and Fanned, the absence of claws is seen in some species, most notably those in Basal, these species of gecko are basally padded, as their toepads are comprised of undivided lamellae across the base of the digit in its entirety. The species in the Basal category have the highest proportion of claw loss, compared to the other toepad types, with 26% of species in Basal having no claws, then 22.7% and 11.1% for Leaf-Like and Fanned, respectively. The species in Leaf-Like, Paired Division and Fanned all possess vertically divided pairs of adhesive toepads with their claws positioned between

these pads at the distal end of their digits. Refer to Fig.6 for toepad type reference images. However, these toepads vary in shape and number between groups, with Leaf-Like and Fanned only having one pair of toepads and Paired Division having more than 2 pairs. The absence of claws seen in Basal, Leaf-Like and Fanned, could suggest a trend towards their loss in geckos with adhesive toepads like these, i.e., one pair of adhesive pads or one undivided adhesive area. As stated by Alturk and Khanoon (2020), more research is need into the effects of claw loss on geckos with adhesive toepads, to better understand why this is happening, and what functional improvements, if any, can be seen. Zhuang et al., (2018) state that adhesive padbearing lineages of geckos have shorter digits, on average. Zani (2000) states that a decrease in digit length increases clinging performance. Therefore, if future research into claw loss in geckos is expanded to researching the morphological trends of digit length, whilst also considering phylogeny, this could provide further information as to why some lineages of gecko have higher rates of claw loss than others. Along with more ecological information to see if there is any correlation with habitat. Plus, understanding every aspect of gecko adhesion can only help to further improve the current bio-inspired techniques and materials that are being developed by material scientists through interdisciplinary research (Russell *et al.,* 2019). In addition, more insight is needed on those species with Paired Division, as none observed in this study exhibited any claw loss. Having more information on their habitat type(s) and what the trends are in each genus within this morphological group of geckos could further explain this lack of claw loss. To the best of my knowledge this is the first time this group has been given a morphological distinction based on its toepad morphology, beyond 'leaf-like', which is typically used to describe all adhesive pad-bearing geckos with a vertical division of the toepad.

Genus-specific Trends:

During data collection some genus-specific trends were spotted regarding digit formation and claw presence. In the case of the *Gehyra* genus, the first toe was lacking a claw but possessed an adhesive toepad, across all four species observed in this study. Interestingly three of the four species were grouped into Paired Division, which might show the beginnings of claw loss in species with this toepad type, or a lack of claws to begin with, via Apoptosis. The other species was placed in Basal, showing that the trend of claw loss, but not complete absence, transpires across toepad morphologies within this genus. It would be interesting to see if geckos in this genus possess any of the other toepad morphologies identified in this study, to see if it's possible for there to be more than 2 types of toepad morphology displayed by the species within a genus. As this study has only come across 2 or less toepad morphologies displayed in each genus analysed (Fig. 19). These species were also found in varying habitat types (Cogger, 2014). More studies into whether this trend is seen across all species in this genus could be beneficial for understanding whether claw loss is a phylogenetic adaptation into successfully occupying ecological niches in varying environments.

The *Lygodactylus* genus showed a reduction in the size of the first digit, lacking an adhesive toepad but possessing a claw, in all seven species observed in this study. All are considered to have Paired Divison, and all are found in vegetation habitats (General Habitat: Tree) aside from one, which is found in saxicolous habitats. Again, there is a need for more study on this genus, to determine how and why the morphology observed in these species evolved. This can be done by categorising toepad morphology in a more detailed manner and noting the species' microhabitat(s) to discover relationships, if any. The *Phelsuma* genus also showed a reduced first digit across the 12 species analysed in this study, all of which lacked a claw and an adhesive toepad on this digit. Notably, the fully formed digits with adhesive toepads varied in their claw possession, between species in this genus. Further in-depth analyses of this genus could determine whether the claw loss observed in this study was due to individual loss, i.e., the individual geckos observed had lost their claw(s), or if it is a species and/or genus wide morphological trait and trend (Russell & Bauer, 2008). As it is

known that across the *Phelsuma* genus all claws are functionally redundant, therefore is this the beginning of the evolutionary stages of total claw loss across this genus?

Claw and Toepad Morphology:

The species in this data set were grouped by their toepad morphology to determine whether there was a relationship with claw morphology. Fig. 8 depicts the mean representative values of claw height, length and width of 56 gecko species observed in this study. Whilst their overall claw size varies, claws on specimens in Basal, Leaf-Like, Non-Adhesive and Paired Division have a common structural, morphological pattern, with length being the largest measurement, followed by height, then width. The Fanned category does not follow this trend as the claw height is the largest measurement, followed by length, then width. This is an interesting result as it suggests a similarity in claw structure across species and genera of gecko, despite variation in toepad morphology. Aside from geckos in Fanned, irrespective of toepad morphology, basic claw structure is constant. Statistical significance was found for claw length, width and height. One potential explanation for this is that the error bar for claw height for the species in Fanned, was very large. This is most likely due to a smaller sample size (9 species) skewing the result. This is an example of how not having, available and distinct toepad morphology data, is hindering current morphological research, and why more accurate and less broad morphological data needs to be catalogued. More in-depth phylogenetic consideration could also help determine if the results for Fanned can be relied upon as all 9 species are from two genus'. This ultimately could have biased the current results shown. A larger sample size could help to prove/disprove the validity of these results. Geckos with Leaf-Like toepads have the smallest claws overall (Fig. 8), this is expected and therefore proved the hypothesis, that arboreal geckos would have a reduced claw size compared to those that are ground dwelling (Non-Adhesive) as they can also rely on their adhesive toepads for climbing (Russel and Gamble, 2019), correct. Also, the species in this category are one of the lightest, on average (Fig. 10), therefore it is logical to assume that they do not need to rely on both their adhesive toepads and claws as the large safety factor of the adhesive toepads most likely generates enough attachment force to allow the lightweight geckos to climb safely and successfully (Russell and Johnson, 2014).

This same hypothesis was partially proved incorrect as, whilst those in Leaf-Like, on average, have the smallest claws, those in Basal, an adhesive toepad category, have the largest claw size, on average, after being logarithmically size corrected (Fig. 8). All other adhesive toepad categories follow the hypothesised trend of having a smaller claw size in comparison to those that lack adhesive toepads (Non-Adhesive). Given that Basal is the only category to produce unexpected results, detailed phylogenetic analysis would be valuable to conduct, in future studies, as these results could have a phylogenetic explanation i.e., the basally padded geckos analysed in this study are showing similar morphological results, as they are closely related. Or that there are valid statistically significant differences in the claw size of basally padded geckos. To improve the reliability of the results of this study, more accurate images of live specimens, would need to be used i.e., those that capture the claw perpendicular to the camera to reduce foreshortening of the claw, and therefore noting inaccurate data. The image data used in this study was not originally collected with claw morphology in mind, therefore it has some inaccuracies in the way the specimens were photographed. Also, using live specimens in replacement of museum ones, could reduce the chances of degradation of the specimen and therefore increases the accuracy of the data logged. This study used a combination of both live and preserved specimens.

The Leaf-Like species also have the least curved claws (Fig. 9). This is unexpected as it was hypothesised that the ground dwelling geckos, Non-Adhesive, would have the straightest claws (Birn-Jeffery *et al.,* 2012) as they aren't needed for climbing steeply inclined substrates which, typically, require claws with an increased curvature, to increase the strength of the claw, which in turn assists with climbing shear surfaces (Zani, 2000). This leads to question the true functionality

of the claws of geckos with this toepad morphology. Fig. 18 shows that geckos with Leaf-Like toepads are seen in a variety of habitat types. Therefore, at least preliminarily, this does not seem like an adaptation to living in a single habitat type, or only encountering similar microhabitat substrates. It would be interesting to see, in future studies, if this is a trend seen across genus' with this toepad type, and what are the phylogenetic relationships between those genus', if any. If trends towards straighter claws are seen, it would also be interesting to see if there are any trends towards claw loss, within this toepad category, as shown in Fig. 8, they have the shortest claw width and height, and the second shortest claw length. Therefore, at least from what is currently available in the literature, these claws aren't functioning as efficiently as what is expected from that of an arboreal gecko.

This same hypothesis regarding arboreal geckos having an increase in claw curvature in comparison to ground dwelling (Non-Adhesive) geckos (Birn-Jeffery *et al.,* 2012) was also, however, proven correct, as the arboreal species in the Fanned toepad category had the most curved claws of all the species analysed (Fig. 9). The other arboreal toepad morphological groups, Basal and Paired Division, also show an increase in mean claw curvature, in comparison to those that are ground-dwelling (Non-Adhesive). The high curvature result for Paired Division is expected as Fig. 7 shows that, of the species analysed in this study, none exhibited any claw loss. Therefore, they seem to rely on their claws, as well as their adhesive toepads, when climbing, and would need an increase in claw curvature, to increase their clinging performance. What is interesting is that Fig. 7 shows that the species analysed with Basal adhesive toepads had the highest rate of claw loss, yet they have the third highest curvature (Fig. 9). Therefore, more research is needed into the claw morphology of geckos with Leaf-Like adhesive toepad type, to determine if this significant result is reliable. As they are the only adhesive toepad category to not follow the expected results. Given that there are over 1500 species of gecko, globally, this data set only tested the claw curvature of 3% of the current known species. With further research and a more formal, detailed system of cataloguing gecko toepad and claw morphology, within the scientific community, more conclusive results can be drawn. More phylogenetic study would also determine if the unexpected Leaf-Like results are due to close relatedness of the species in this study. As some genus' are closely related and therefore would share very similar morphological traits (Fig. 19). Also, using images with a more accurate imaging angle will allow for more reliable data collection, by reducing the chances of the images foreshortening the claw and therefore increasing the curvature angle.

Body Weight and Toepad Morphology:

I did not find support for my hypothesis that ground dwelling geckos, i.e., those that have Non-Adhesive toepads and can only climb to the capacity in which their claws allow, due to the maximum load bearing capacity of adhesive toepads (Labonte and Federle, 2015), would be the heaviest. With a statistical significance of $p= 0.002$, this hypothesis was proved incorrect. The gecko species categorised in Fanned, due to having fan-like adhesive toepads, with a vertical division separating the two pads, which are comprised of lamellae; either increasing or decreasing in length from the distal end of the digit to the base, were, on average, the heaviest, with those in Paired Division being the lightest on average; those in Leaf-Like's lower weight range were the lighest overall (Fig. 10). On average, the mean weight of those in the Non-Adhesive toepad category was the second lightest of all five categories analysed. The lightest species in the Fanned category's weight range is only marginally lighter than the heaviest species in the Non-Adhesive's (ground dwelling) weight range (Fig. 10). Showing that, the species analysed and considered ground-dwelling, in this study, are much lighter than previously assumed. Post Hoc Tukey tests found statistical significance between the mean weight of the arboreal species in the Fanned category and that of the species in the Paired Division, therefore between the heaviest and lightest categories (Fig. 10).

One potential reason for this ability to overcome a large body weight while continuing with an arboreal lifestyle is seta position, therefore lamellae position, and placement on the toepad itself (Russell and Johnson, 2014). Russell *et al.* (2015) found that the *Gonatodes* genus is a good representative of an intermediate toepad structure between that of a ground-dwelling gecko with no adhesive toepads and an arboreal one with adhesive toepads. This suggests that more research into toepad structure and morphology and how this correlates with body weight and/or size, would give a better opportunity to discover the answers to the questions the results from this study have brought up. For example, is overcoming a large body weight due to seta position? Or toepad morphology? Or lamellae number? Or a combination? This is also where using phylogeny is useful. The species in Fanned come from two genus', *Ptyodactylus* and *Uroplatus,* Fig. 19 shows that neither of these genus' are closely related. Yet all the species analysed in this study, from those genus', have the same toepad morphology and all have a heavier body weight in comparison to most of the other species in this study (Fig. 10). These species also had a larger claw height measurement (from dorsal to ventral side at the base of the claw), compared to their claw length and width (Fig. 8) in addition to having the most curved claws (Fig. 9). This large claw height could be a morphological adaptation to help counter a large body weight and stabilise the individual when climbing. Having a larger base to the claw in comparison to the length, could allow the claw to endure more stress, induced by a higher body weight, without the risk of breakage, compared to a claw with a smaller height having to manage the same weight load (Zani, 2000).

The claw of the geckos in the Fanned category sits between the two toepads at the distal end of the digit. This claw positioning could act like an anchor to increase the clinging force exhibited by the individual when climbing inclined surfaces. It is known that some species of arboreal geckos possess claws to assist the adhesive toepad(s) with climbing, by increasing clinging force on rough surfaces (Naylor and Higham, 2019). Therefore, given the claw morphology of the species' with Fanned toepads it is worth further researching whether these morphological traits have evolved to also help counter the large body weight (Fig. 10) of these gecko species and allow them to maintain an arboreal lifestyle. The number of species analysed in Fig. 10 is 148, whilst this is a good starting point, for future research more data is needed to strengthen the validity of the significance of this result. In addition to more phylogenetic consideration of the species in each category. As Fanned only contained nine species from two genus'. Therefore, this could bias and skew the results towards Fanned being the heaviest group due to a small number of species, whereas using a larger species count could either further prove or disprove the accuracy and reliability of this result.

Toepad/Claw Morphologies as Predictors for Body Weight:

Linear regressions were carried out on the morphological measurements collected from toepad and claw images for multiple species, to find out if they can be used as an indicator for gecko body weight. The 'Width' of each toepad was taken by measuring the width of the toepad, horizontally, for all five 'Toepad Types' (Fig. 11). After size correction a strong relationship was found between toepad width and body weight (r^2= 0.449) which shows that this proportional measurement is a useful predictor for body weight. Observationally, the heavier geckos are easier to predict their weight based on their toepad width. The 'Gap-Width' measurement was taken by measuring the width of the gap between the one or more pairs of toepads in arboreal geckos in the groups comprising of Leaf-Like, Paired Division and Fanned, caused by the vertical separation of the pads. After size correction, a strong relationship was found when gap-width was plotted against body weight (r^2=0.395) (Fig. 12). This shows that the proportional toepad gap-width measurement is a useful predictor for body weight. The species with the mid-range body weights analysed in this regression, were the easiest to predict their weight, based on the toepad gap-width. Of all the toepad morphological regressions carried out, this regression had the smallest sample size, 61 species, perhaps with more data this relationship will strengthen, considering there are over 1500 known

species of gecko (Zug, 2020). Currently, the above results show that these morphological characteristics are useful predictors for body weight as they scale with body size. It would be interesting to see if this scaling remains true for species/individual geckos that have a much larger/smaller body weight than expected. As previously stated by Russell and Johnson (2014) and Labonte *et al.* (2016), toepad size scales isometrically rather than allometrically, after a given body size. Afterwards the adhesive toepads overlap and become functionally useless. Also, it would be interesting to see if the same scaling pattern is seen with claws, and if there's a limit to their size before functional redudnacy is reached. The 'Lamellae Number' was taken for each of the 83 species analysed by counting each row present on the toepad of the fourth hind or front foot of each gecko, for continuity. A strong relationship was found between the lamellae number of adhesive padded geckos and their body weight (r^2=0.361) (Fig. 13). This suggests that lamellae number is a useful predictor for body weight. Perhaps the reason for this is that heavier geckos need more lamellae to help increase clinging force to compensate for a large body weight. Further study with a larger sample size, and larger weight range would be needed to test this. For more reliable results, in future, a PGLS would need to be carried out alongside the regressions, to see if the predictability of body weight based on these morphological characteristics is due to the phylogenetic relatedness of the species analysed for each regression during this study, or not.

A strong relationship was found between body weight and the size corrected claw measurements for length, width and height (Fig. 14, 15 and 16). The data collected for these regressions came from a relatively small number of species for each measurement, 56 species for all. Once again this demonstrates that using these proportional measurements as predictors for body weight, is useful given the high r^2 values (0.329, 0.361 and 0.416 respectively). As with the toepad morphological measurements, for more conclusive results in future, PGLS's would need to be ran for these regressions also. Collecting a larger data set may prove fruitful in discovering a stronger relationship between both the toepad and claw measurements and body weight, in the future. It would reduce the chances of phylogenetic relatedness influencing the results. If these results were mirrored or strengthened when using a larger sample size, which includes species from more genus', then it would diffinitively prove relationships between toepad and claw morphological measurements and body weight. A study on Liolaemini lizards, which are terrestrial and heavy bodied in comparison to most geckos, showed a positive correlation between claw height and clinging performance on rough surfaces (Tulli *et al.,* 2012). Perhaps with the addition of adhesive toepads in geckos, this could help explain why the heavier species in Fanned (Fig. 10) are able to maintain arboreality. If a relationship is found between claw height and body weight in future studies, it could help to provide scientific proof to back up this assumption, as well as providing further evidence that increases the validity of the results shown in Fig. 10 and Fig. 16.

Body Weight and General Habitat Occupation:

The mean weight of the 236 species of gecko that live in each 'General Habitat' type: Ground, Multi, Saxicolous and Tree was analysed (Fig. 17). The general habitat category 'Tree' covered any forest or vegetation microhabitats where the different species live, including those that are manmade, e.g., agroforests. This also grouped together species that lived at different elevations within these habitats. The species in the 'Tree' category were observed to be the heaviest, on average, with most of these species being arboreal (Fig. 18). This is an unexpected finding because, as stated previously, it was assumed that the heaviest geckos would be those that are ground dwelling (Non-Adhesive). Due to the aforementioned size limits on equal load sharing across adhesive toepads, plus the morphological size constraints on increasing the adhesive toepad size (Russell and Johnson 2014: Labonte *et al.* 2016: Labonte and Federle, 2015). Therefore, any gecko which is heavier than these limits was assumed to have to be ground dwelling. Fig. 17 did not show

any statistical significance, meaning no relationship between Weight and General Habitat was found; therefore, the results can only be interperated in an observational, preliminary fashion.

Fig. 18 however, did result in statistically significant findings. This result showed that there is a significant relationship between toepad morphology and habitat type, at the general level. Only 9 of the species in the 'Tree' category are ground dwelling and classified with Non-Adhesive toepads, compared to 53 species being arboreal and classified with Basal, Leaf-Like, Paired Division or Fanned toepads: with 25 of these species having Basal toepads (Fig. 18). This finding shows that the majority of species of arboreal geckos that live in 'Tree' habitats are basally padded. This is interesting as given the high rate of claw loss in the basally padded geckos analysed in this study, this further emphasises the need for more in-depth ecological data to be collected and analysed. Especially microhabitat data, as this could help depict the types of substrates, therefore the topographies, in which these geckos come into contact with. Which could explain their lack of need for claws, if the substrates are smooth and/or at low inclines (Naylor and Higham, 2019).

The 'Ground' category grouped together species found in varying ground-type microhabitats, e.g., desert and savannah et cetera. It is comprised of species from Basal, Leaf-Like, Non-Adhesive and Paired Division; no species with Fanned toepads were present in these habitats. This is an interesting finding, as previously stated in Fig. 10, the individuals in this group (Fanned) were among the heaviest species. The heaviest species were presumed to have been found in the 'Ground' habitats, as it was assumed that the ground dwelling geckos (Non-Adhesive) would be the heaviest species. Once again, this reiterates that the arboreal geckos are reaching heavier body weights than previously assumed, in comparison to those that are ground dwelling (Birn-Jeffery *et al.,* 2012).

The geckos in the 'Multi' general habitat category were placed in this habitat type if they were found in 2 or more varying microhabitat types. 26 of the species in this category were arboreal compared to 11 that were ground dwelling, showing that, of the species analysed in this study, there were more arboreal species that were able to adapt to varying microhabitat types compared to the ground dwelling species (Fig. 18). Implying that being arboreal is to be less specialised than being ground dwelling, arboreal geckos potentially encounter a wider variety of substrates when climbing through their environment(s) (Vanhooydonck *et al.,* 2005); whereas ground dwellers, may only encounter a limited number of different substrates, making them more specialised. This may be coincidental or could prove to be significant with further research into habitat adaptability, at the micro level, as well as the consideration of toepad morphology.

There is no statistically significant difference in body weight between geckos living in different general habitat types (Fig. 17). Whilst not significant I believe it is worth further researching, with a larger data set and potentially more rigorous testing, to discover if a significant relationship is found as it could show that many arboreal geckos living in tree/vegetation habitats are heavier than those in different ground-type habitats. The next step after this would be to record their microhabitats to see if there is a relationship to weight, alongside further research into the toepad types of the species in these microhabitats to discover any potential relationship.

Gecko species with Basal, Leaf-Like, Non-Adhesive and Paired Division toepad types can be found in all 'General Habitat' types (Fig. 18). Fanned was the only morphological category that was only found in two of the four habitat categories: Saxicolous and Tree. The data for the species in Fanned comes from species belonging to 2 genera; 1 found in saxicolous habitats the other in forests. The locations where the 2 genera were found were Israel and Madagascar. This geographical divide makes it impossible to speculate as to any pattern in their adaptability to differing environments. This means that there could be species that would be categorised as having the toepad morphology

for Fanned, capable of living in multiple different environments and therefore being placed into the 'Multi' category, this data set simply doesn't have them. This suggests that more research is needed into the habitats in which the geckos with this toepad morphology reside, at the micro level. As this group of species are the heaviest, on average (Fig. 10), and arboreal, it would be useful to know at what elevation level and inclines these species are typically found. This would help us to better understand what effect, if any, their large body weight is having on how they interact with their environment. For example, does it stop them from reaching certain inclines, because perhaps arboreality becomes unstable due to such a large weight? Also, is this the reason why they were not found in 'Ground' type environments, in this study; because their large weight means they move slower, as seen in a study by Zamora-Camacho *et al.* (2014) in a non-gekkonid lizard *Psammodromus algirus*. Therefore, meaning that they're at a greater risk of predation at lower elevation levels?

Body Weight and Microhabitat Occupation:

The number of species in each microhabitat type and their toepad morphology was analysed (Fig. 20). Unfortunately, due to a lack of information regarding geckos' microhabitat types, the statistical conclusions from this result, X= Chi Square Test, 6 df, p= 0.020, couldn't be relied upon as the data did not meet the test assumptions. This data set also contained a relatively small number of species (n=148), when compared to the total number of gecko species (1500+ (Zug, 2020)). However, as a preliminary data set, the results are interesting. One interesting feature is that the geckos with Leaf-Like and Fanned toepads are found in a much smaller array of microhabitats in comparison to the other groups, with Basal toepads being found in the greatest number of different microhabitats. This is different to what was expected, as it was hypothesised that arboreal geckos with Leaf-Like adhesive toepads would occupy a wider range of microhabitats than those with basal toepads. This was formed off the basis that the same species of gecko with Leaf-Like adhesive toepads have been observed in multiple microhabitat types in comparison to a basally padded gecko on the same island (Russell & Delaugerr, 2016). From this it appears as though geckos that are basally padded are therefore the most adaptable, although much more data is needed from a larger number of gecko species to determine if this initial preliminary result is true. This highlights a current gap in the literature as there is little data available regarding geckos' microhabitat occupation. More microhabitat information is needed to be collected and/or recorded in future research, to allow for more in-depth comparative analysis research to be conducted; to better understand if there are any links to morphology, that allows them to fulfil ecological niches, in varying ways; spatial, temporal or trophic (Petford & Alexander, 2020).

Chapter 2

The aims of this chapter were to create a small-scale Finite Element Analysis of the claw structure of representative gecko species from each 'Toepad Type', to discover if there were any preliminary links between claw morphology and habitat use, at the general and micro level. Whilst also seeing if there is any evidence to suggest that claws help to compensate for a larger body weight in arboreal geckos, by providing additional support to the adhesive toepads, with their shape and structure.

2-dimensional stress contour maps of the claws, showing the area(s) most and least susceptible to breakage due to stress, for each representative species for each 'Toepad Type', were created (Fig. 21). Of the arboreal toepad types, representative claws for Basal (*Hoplodactylus duvacelii*) and Leaf-Like (*Phyllodactylus lanei*) are similar morphologically, in that they both have very small areas that's most prone to breakage, both at the very tip of each claw. They, therefore, seemingly have the 'strongest' claws as, in comparison to the others, their 'weakest' areas are the smallest. This could be advantageous as, if any breakage was to occur, only the tip of the claw is likely to be damaged, leaving the rest intact. Therefore, the animal would only have to wait for their claw to

grow a small amount in length in that area, via cell proliferation that is present across the entire reptilian claw (Alibardi, 2009), before being back to a normally functioning state, as opposed to damaging a larger portion of the claw and having to wait longer for it to repair. Waiting longer could impair the individuals climbing ability/safety factors when climbing, and/or hunting/predator evasion capacity. Also, breaking a larger section of the claw risks breakage beyond the base of the claw, which risks the claw regenerating in a reduced size, known as a stub-claw (Alibardi and Meyer-Rochow, 2021); or potentially not regenerating back at all. This would also, presumably impair the geckos' climbing ability/safety factors when climbing as it would now have a claw that is reduced in size or potentially a reduced total number of claws. Both claws representing these toepad types also have similar curvatures (132°, 140° respectively) and both representative species are categorised in the "Multi" general habitat grouping, with similar microhabitats. The deformation plots show that both these claws have a limited range of movement, this most likely helps improve the geckos' stability when using its claws, alongside its adhesive toepads, for climbing. With further research into gecko ecology and toepad and claw morphology, it would be possible to determine whether these similarities in claw shape and structure are seen across species and/or genera with these toepad types, and potentially discover the reasons for this. Is it due to habitat type and therefore daily wear and shape change due to substrate impact (Pamfilie, 2020), phylogeny, toepad morphology, all three or something else entirely?

The contour map for the representative claw for species with Non-Adhesive toepads, *Salutarius cornutus,* shows it has the largest area susceptible to breakage. This was hypothesised as it was thought that the claws of adhesion assisted arboreal geckos would redirect forces to a single point along the claw, reducing the area of the claw most susceptible to breakage, due to their need for their claws to assist them during vertical climbing. Gecko claws whether they possess adhesive toepads or not, are directional with an inter-locking clinging mechanism (Arnold, 1998; Cartmill, 1985; Zani, 2000). Given that non-adhesive toepad geckos mainly rely on their claws when climbing, this claw shape being the "weakest" of all the claws tested during this project, highlights their claws reduced function as a climbing "tool", in comparison to arboreal geckos with adhesive toepads. Especially when considering that ground dwelling geckos do not have an adhesive system to use as back-up if their claw(s) were to break, when climbing. This contour map shows this claw shape's lack of suitability for climbing, as it likely provides less stability, in comparison to the other claw shapes; potentially a reason why many ground dwelling species have a limited climbing capacity. Along with many ground dwelling species having a shorter claw height and reduced curvature, as an increase in these morphological traits is known to increase clinging performance on rough surfaces (Zani, 2000). A lack of information regarding reptilian claw morphology and claw use in their natural environments, as mentioned by Thomson and Motani (2020), is a hindering factor in allowing for a better understanding of why geckos claws are shaped the way they are. Schwarz *et al.* (2021) discusses the intraspecific plasticity that allows for adaptability to varying microhabitat types, in the gecko species, *Mediodactylus kotschyi.* This species would be categorised as ground dwelling in this project as it does not possess adhesive toepads, therefore, only capable of climbing to the capacity in which its claws allow. However, it showed phenotypic changes to the varying habitats across several Greek islands (ibid.). The allopatric adaptations shown between populations were that those occupying more saxicolous environments, had taller but shorter claws, in comparison to the longer claws exhibited by population that live in tree habitats on the same or separate island(s)(ibid). The change in claw length has allowed for adaptation to changes in substrate/habitat and the increase in claw height, as previously stated by Zani (2000), has increased the clinging performance of the claw on rough substrates. This is an example of the benefits of being a generalist rather than a specialist (Schwarz *et al.,* 2021). This example demonstrates the need for further research into microhabitat occupation, to determine if any morphological trends are

present, e.g., claw size, curvature. Whilst considering link to toepad morphology and the possession of an adhesive system or not.

Salutarius cornutus' movement range is seemingly different from that of the claws representing the other toepad types as it only appears to have movement at the tip of the claw, whereas the deformation plots for the other claws analysed show movement at the tip and base. This lack of movement capacity at the base of the claw could be why these claws are better suited to foraging behaviours such as digging, rather than climbing. A lack of movement at the base, would make digging more efficient, whereas for climbing, a small range of movement may be needed to remain stable when climbing rough substrates, as this could help to counter any instability within the substrate and remain attached. However, a claw with more rigidity to its movement may not be able to counter such instability and it could either break and/or cause the animal to fall. The representative species for Non-Adhesive toepads live in forested habitats, meaning that its claws are likely used to manoeuvre through and over lightweight, soft substrates like forest debris of varying kinds, e.g., leaf litter. That makes this the perfect claw shape and structure for foraging and locomotion behaviour such as this, as these types of substrates are unlikely to cause breakages to the claws.

An example of morphological adaptation from the same genus is the species *Saltuarius salebrosus,* again this species has non-adhesive toepads, and solely relies on its claws when climbing. It is noted by Zhuang *et al.* (2019) that this species has highly symmetrical digits, which is typically seen in adhesive pad-bearing geckos, this could be an adaptation to maximise clinging performance of the claws, when climbing. This highlights the need for further research into gecko morphology and the relationship between claws and toepads to maximise clinging performance. Again, whilst considering any links to microhabitat type.

The representatives of Paired Division and Fanned toepads, *Lygodactylus chobiensis and Ptyodactylus guttatus* respectively, also have similarities in their claw structure. They are similar in that they are the most curved claws out of the five representatives, with curvatures of 107° and 93° respectively. The deformation plots both have movement at the tip and base of the claw. Their areas that are the most susceptible to breakage are similar too, comprising at the tip of the claw. Phylogenetically these species, however, are distantly related (Fig. 19). *Ptyodactylus guttatus'* claw, like *Hoplodactylus duvacelii* and *Phyllodactylus lanei*, shows an area of weakness at the base of the claw also. Although the size of the area of weakness on the claw of *Ptyodactylus guttatus* is larger than on the other two. The *Ptyodactylus* and *Phyllodactylus* are closely related (Fig. 19), therefore their similarities in claw structure in unsurprising, this also explains similarities in their adhesive toepad structure, *Phyllodactylus lanei* having Leaf-Like toepads, and *Ptyodactylus guttatus* categorised as having Fanned toepads; as both toepad types display vertical division of the adhesive toepad, resulting in a mirror-image pair of adhesive areas. However, Hoplodactylus is distantly related to both genus', and has Basal toepads. Showing a possible claw morphological characteristic that occurs across toepad types. The placement of the weaker area is a surprising find, as these species are all arboreal and having a 'weak' area at the base of the claw leads to questions regarding the stability and strength of these claws, considering that they are used when climbing sometimes vertical surfaces. This is particularly interesting as *Ptyodactylus guttatus* is known for being a specialised climber, in regard to climbing vertical surfaces (Ali *et al*., 2018). Also, the Fanned toepad group were found to be the heaviest, on average (Fig. 10), therefore it is assumed that their claws would be placed under more stress due to a higher body weight. Meaning that, of all the species studied in this data set, the claws of the Fanned toepad geckos should be the strongest and have the smallest areas most susceptible to breakage. More research is needed into gecko claw morphology and the mechanics of their use in arboreal species to better understand why these

'weak' areas occur without, seemingly, hindering geckos' movement and stability when climbing, especially when factoring in body weight. The small sample size and time constraints of this project did not allow for more thorough research to be conducted on a larger scale, to investigate if finite element analyses could provide better insight into any trends and/or relationships between gecko claw structure and toepad type and/or habitat.

One difference in structure between the claws of *Lygodactylus chobiensis and Ptyodactylus guttatus* is that *Lygodactylus chobiensis* has, visually, a significantly larger area that is more susceptible to breakage, covering most of the length of the claw. This is an unusual find as it was hypothesised that an increase in curvature would redirect forces to a single point along the claw, reducing the area susceptible to breakage, and that this would be seen in arboreal geckos, as it would allow the 'stronger' areas of their claws to endure an increased stress load, that would aid them in climbing vertically. Given the large 'weak' area of *Lygodactylus chobiensis'* claw, and the proportion of the claw it covers, it is surprising that this gecko is arboreal and manages to successfully climb. However, *Lygodactylus chobiensis* is categorised in Paired Division, this group, on average, had the second most curved claws (Fig. 9) and were the lightest toepad group (Fig. 10). An increase in curvature increases clinging performance for geckos, when climbing (Zani, 2000) therefore perhaps this morphological trait along with a lighter body weight (12.3g) compensates this species for having a claw with a proportionally large area that is most susceptible to breakage. Also, the tip of *Lygodactylus chobiensis'* claw is much more rounded than any of the others (Fig. 22). This makes sense when considering that their habitat is the forest floor, among the debris. Many of their substrates are soft and easy to manoeuvre through, so they would have no need for stronger, sharper claws. However, it may be a characteristic of the individual gecko observed and not species-wide, therefore a greater sample size is needed to determine the true reasoings behind this feature. *Ptyodactylus guttatus*, lives in saxicolous, semi-desert habitats and is therefore in need of a stronger, sharper claw to move through the rocky environment. Fig. 21 shows that, while sharper than *Lygodactylus chobiensis'* claw, *Ptyodactylus guttatus'* claw is neither as sharp and pointed like that of *Salutarius cornutus* or rounded like *Lygodactylus chobiensis,* it's more intermediary in its sharpness. It would be interesting to know if this is a morphological adaptation or simply general wear and tear of this individual gecko's claw, from living in a saxicolous habitat. As it is known that claws become ineffective at aiding in clinging performance, once the substrate protrusion is larger than the distance between the claw tip and the most curved point of the subunguis (Song *et al.,* 2016).

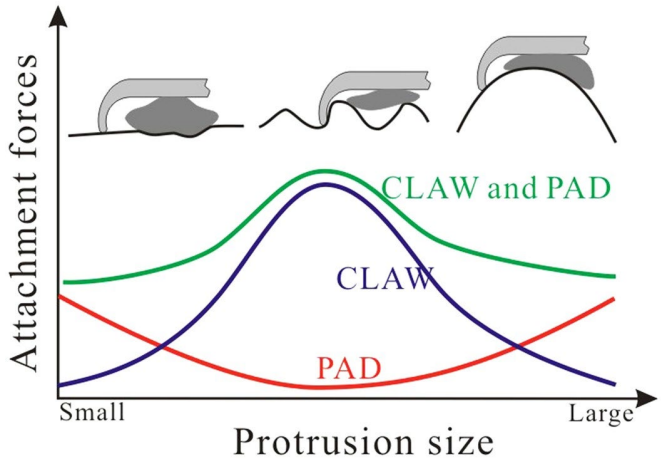

Figure 22: Diagram showing the effects of different sizes of substrate protrusions on claw attachment (Song *et al.,* 2016).

Therefore, developing claws with the most effective curvature and claw tip size is advantageous for geckos to survive in their natural habitats. This highlights a weakness of this study, its small sample size, due to the lack of available microhabitat data, as a larger scale data set would allow for a more in-depth comparisons to be made regarding claw shape and structure, when considering toepad type and relating this to microhabitat. more research is needed on a larger variety of species with all five toepad types, and a range of microhabitats, to determine if these reasonings behind the claw morphology of the representative species have any validity (Thomson and Motani, 2020).

Conclusion

Gecko morphology is varied, from body weight to toepad type to claw size (height, length, width, and curvature) and claw presence or reduction or total absence. The variation in adhesive toepad types allowed for further categorisation, beyond the basic 'basally padded' and 'leaf-like' groupings, to show more accurately the different morphologies. Habitat type also varies considerably across the Gekkotan suborder, which is why it is important for future studies to note each species' microhabitat in addition to their general habitat type. If future studies include more detailed morphological and habitat information, then the significant findings of this study can be built upon. This is particularly true for future studies analysing gecko microhabitats, as detailed information in the published literature is not currently widely available. This ultimately limited the habitat data used in this study to the general level. However, the microhabitat data found and used did produce some interesting preliminary results when compared to toepad type. Claw reduction and/or partial or total loss seen in some species and across some genus of gecko may also be better understood, and the significant results found in this study further explained, with more detailed ecological information being published in the future. Along with linking this to phylogeny to better understand the core reasonings behind these evolutionary morphological adaptations. A large-scale Finite Element Analyses of gecko claws would help to understand the morphological and structural differences between gecko species, which were observed in the small-scale analyses in this study; whilst also uncovering if these differences can be linked to toepad type and/or habitat occupation.

Appendices

Appendix 1

Table 1: Supplementary body weight data for the species included in or added to, the main species list formed from the data in Meiri (2010) and Kulyomini *et al.* (2019).

Species	Reference
Amalosia rhombifer	Riedel, J., Vucko, M.J., Blomberg, S.P., Robson, S.K. and Schwarzkopf, L., 2019. Ecological associations among epidermal microstructure and scale characteristics of Australian geckos (Squamata: Carphodactylidae and Diplodactylidae). *Journal of Anatomy*, *234*(6), pp.853-874.
Carphodactylus laevis	Riedel, J., Vucko, M.J., Blomberg, S.P., Robson, S.K. and Schwarzkopf, L., 2019. Ecological associations among epidermal microstructure and scale characteristics of Australian geckos (Squamata: Carphodactylidae and Diplodactylidae). *Journal of Anatomy*, *234*(6), pp.853-874.
Chondrodactylus turneri	Barabanov, V., Gulimova, V., Berdiev, R. and Saveliev, S., 2015. Object play in thick-toed geckos during a space experiment. *Journal of Ethology*, *33*(2), pp.109-115.
Crenadactylus ocellatus	Withers, P.C., Aplin, K.P. and Werner, Y.L., 2000. Metabolism and evaporative water loss of Western Australian geckos (Reptilia: Sauria: Gekkonomorpha). *Australian Journal of Zoology*, *48*(2), pp.111-126.
Dactylocnemis pacificus	Gartrell, B.D., Ahn, J.Y., Khude, R., Dougherty, N., Johnson, K., McCutchan, J., Clarke, A. and Hunter, S., 2020. Thermal burns of the spectacle associated with supplementary heating in native New Zealand geckos. *New Zealand veterinary journal*, *68*(2), pp.126-133.
Diplodactylus alboguttatus	Withers, P.C., Aplin, K.P. and Werner, Y.L., 2000. Metabolism and evaporative water loss of Western Australian geckos (Reptilia: Sauria: Gekkonomorpha). *Australian Journal of Zoology*, *48*(2), pp.111-126.
Diplodactylus ameyi	Riedel, J., Vucko, M.J., Blomberg, S.P., Robson, S.K. and Schwarzkopf, L., 2019. Ecological associations among epidermal microstructure and scale characteristics of Australian geckos (Squamata: Carphodactylidae and Diplodactylidae). *Journal of Anatomy*, *234*(6), pp.853-874.
Diplodactylus ornatus	Withers, P.C., Aplin, K.P. and Werner, Y.L., 2000. Metabolism and evaporative water loss of Western Australian geckos (Reptilia: Sauria: Gekkonomorpha). *Australian Journal of Zoology*, *48*(2), pp.111-126.

Diplodactylus platyurus	Riedel, J., Vucko, M.J., Blomberg, S.P., Robson, S.K. and Schwarzkopf, L., 2019. Ecological associations among epidermal microstructure and scale characteristics of Australian geckos (Squamata: Carphodactylidae and Diplodactylidae). *Journal of Anatomy*, *234*(6), pp.853-874.
Diplodactylus polyophthalmus	Withers, P.C., Aplin, K.P. and Werner, Y.L., 2000. Metabolism and evaporative water loss of Western Australian geckos (Reptilia: Sauria: Gekkonomorpha). *Australian Journal of Zoology*, *48*(2), pp.111-126.
Diplodactylus pulcher	Withers, P.C., Aplin, K.P. and Werner, Y.L., 2000. Metabolism and evaporative water loss of Western Australian geckos (Reptilia: Sauria: Gekkonomorpha). *Australian Journal of Zoology*, *48*(2), pp.111-126.
Diplodactylus squarrosus	Withers, P.C., Aplin, K.P. and Werner, Y.L., 2000. Metabolism and evaporative water loss of Western Australian geckos (Reptilia: Sauria: Gekkonomorpha). *Australian Journal of Zoology*, *48*(2), pp.111-126.
Diplodactylus wiru	Riedel, J., Vucko, M.J., Blomberg, S.P., Robson, S.K. and Schwarzkopf, L., 2019. Ecological associations among epidermal microstructure and scale characteristics of Australian geckos (Squamata: Carphodactylidae and Diplodactylidae). *Journal of Anatomy*, *234*(6), pp.853-874.
Gehyra pilbara	Withers, P.C., Aplin, K.P. and Werner, Y.L., 2000. Metabolism and evaporative water loss of Western Australian geckos (Reptilia: Sauria: Gekkonomorpha). *Australian Journal of Zoology*, *48*(2), pp.111-126.
Gehyra punctata	Withers, P.C., Aplin, K.P. and Werner, Y.L., 2000. Metabolism and evaporative water loss of Western Australian geckos (Reptilia: Sauria: Gekkonomorpha). *Australian Journal of Zoology*, *48*(2), pp.111-126.
Gehyra purpurascens	Withers, P.C., Aplin, K.P. and Werner, Y.L., 2000. Metabolism and evaporative water loss of Western Australian geckos (Reptilia: Sauria: Gekkonomorpha). *Australian Journal of Zoology*, *48*(2), pp.111-126.
Gehyra variegata	Withers, P.C., Aplin, K.P. and Werner, Y.L., 2000. Metabolism and evaporative water loss of Western Australian geckos (Reptilia: Sauria: Gekkonomorpha). *Australian Journal of Zoology*, *48*(2), pp.111-126.
Gekko gekko	Aowphol, A., Thirakhupt, K., Nabhitabhata, J. and Voris, H.K., 2006. Foraging ecology of the Tokay gecko, Gekko gecko in a residential area in Thailand. *Amphibia-Reptilia*, *27*(4), pp.491-503.
Hemidactylus flaviviridus	Parida, P., Ghosh, A.K. and Mohanta, L., EFFECT OF COLD SHOCK ON LIPID PEROXIDATION AND REDUCED

	GLUTATHIONE LEVEL OF THE LIVER OF Hemidactylus flaviviridis.
Hemidactylus garnotii	Irschick, D.J., Herrel, A. and Vanhooydonck, B., 2006. Whole-organism studies of adhesion in pad-bearing lizards: creative evolutionary solutions to functional problems. *Journal of Comparative Physiology A*, *192*(11), pp.1169-1177.
Hemidactylus mabouia	Johnson, S.K., Parmerlee Jr, J.S., Eifler, D.A. and Powell, R., 2013. Comparative water-loss rates of Hemidactylus mabouia and Sphaerodactylus notatus on Eleuthera Island, Commonwealth of the Bahamas. *Herpetology Notes*, *6*, pp.471-475.
Lucasium immaculatum	Riedel, J., Vucko, M.J., Blomberg, S.P., Robson, S.K. and Schwarzkopf, L., 2019. Ecological associations among epidermal microstructure and scale characteristics of Australian geckos (Squamata: Carphodactylidae and Diplodactylidae). *Journal of Anatomy*, *234*(6), pp.853-874.
Lucasium steindachneri	Riedel, J., Vucko, M.J., Blomberg, S.P., Robson, S.K. and Schwarzkopf, L., 2019. Ecological associations among epidermal microstructure and scale characteristics of Australian geckos (Squamata: Carphodactylidae and Diplodactylidae). *Journal of Anatomy*, *234*(6), pp.853-874.
Lygodactylus capensis	Simbotwe, M.P., 1983. Comparative ecology of diurnal geckos (Lygodactylus) in Kafue flats, Zambia. *African Journal of Ecology*, *21*(3), pp.143-153.
Lygodactylus chobiensis	Simbotwe, M.P., 1983. Comparative ecology of diurnal geckos (Lygodactylus) in Kafue flats, Zambia. *African Journal of Ecology*, *21*(3), pp.143-153.
Nephrurus asper	Riedel, J., Vucko, M.J., Blomberg, S.P., Robson, S.K. and Schwarzkopf, L., 2019. Ecological associations among epidermal microstructure and scale characteristics of Australian geckos (Squamata: Carphodactylidae and Diplodactylidae). *Journal of Anatomy*, *234*(6), pp.853-874.
Nephrurus stellatus	Withers, P.C., Aplin, K.P. and Werner, Y.L., 2000. Metabolism and evaporative water loss of Western Australian geckos (Reptilia: Sauria: Gekkonomorpha). *Australian Journal of Zoology*, *48*(2), pp.111-126.
Oedura bella	Riedel, J., Vucko, M.J., Blomberg, S.P., Robson, S.K. and Schwarzkopf, L., 2019. Ecological associations among epidermal microstructure and scale characteristics of Australian geckos (Squamata: Carphodactylidae and Diplodactylidae). *Journal of Anatomy*, *234*(6), pp.853-874.
Oedura cincta	Riedel, J., Vucko, M.J., Blomberg, S.P., Robson, S.K. and Schwarzkopf, L., 2019. Ecological

	associations among epidermal microstructure and scale characteristics of Australian geckos (Squamata: Carphodactylidae and Diplodactylidae). *Journal of Anatomy*, *234*(6), pp.853-874.
Oedura jowalbinna	Hoskin, C.J. and Higgie, M., 2008. A new species of velvet gecko (Diplodactylidae: Oedura) from north-east Queensland, Australia. *Zootaxa*, *1788*(1), pp.21-36.
Oedura reticulata	Withers, P.C., Aplin, K.P. and Werner, Y.L., 2000. Metabolism and evaporative water loss of Western Australian geckos (Reptilia: Sauria: Gekkonomorpha). *Australian Journal of Zoology*, *48*(2), pp.111-126.
Pachydactylus mariquensis	Bauer, A.M., Russell, A.P. and Edgar, B.D., 1989. Utilization of the termite Hodotermes mossambicus (Hagen) by gekkonid lizards near Keetmanshoop, South West Africa. *African Zoology*, *24*(4), pp.239-243.
Pachydactylus punctatus	Bauer, A.M., Russell, A.P. and Edgar, B.D., 1989. Utilization of the termite Hodotermes mossambicus (Hagen) by gekkonid lizards near Keetmanshoop, South West Africa. *African Zoology*, *24*(4), pp.239-243.
Phelsuma mutabilis	Consequence of inter class competition and predation on the adaptive radiation of lizards and birds in the dry forest of western Madagascar
Phyllodactylus delsolari	Reproduction in a gecko assemblage (Squamata: Phyllodactylidae) in the Marañon Region (Peru) and comments on the largest gecko in the New World
Phyllodactylus pulcher	Williams, R.J., Horrocks, J. and Pernetta, A., 2015. Natural history, distribution, and conservation status of the Barbados leaf-toed gecko, Phyllodactylus pulcher Gray, 1828 (Squamata, Gekkonidae). *Herpetology Notes*, *8*, pp.197-204.
Phyllodactylus reissii	Reproduction in a gecko assemblage (Squamata: Phyllodactylidae) in the Marañon Region (Peru) and comments on the largest gecko in the New World
Phyllodactylus thompsoni	Reproduction in a gecko assemblage (Squamata: Phyllodactylidae) in the Marañon Region (Peru) and comments on the largest gecko in the New World
Phyllurus amnicola	Riedel, J., Vucko, M.J., Blomberg, S.P., Robson, S.K. and Schwarzkopf, L., 2019. Ecological associations among epidermal microstructure and scale characteristics of Australian geckos (Squamata: Carphodactylidae and Diplodactylidae). *Journal of Anatomy*, *234*(6), pp.853-874.
Phyllurus nepthys	Riedel, J., Vucko, M.J., Blomberg, S.P., Robson, S.K. and Schwarzkopf, L., 2019. Ecological associations among epidermal microstructure and scale characteristics of Australian geckos (Squamata: Carphodactylidae and

	Diplodactylidae). *Journal of Anatomy*, *234*(6), pp.853-874.
Phyllurus ossa	Riedel, J., Vucko, M.J., Blomberg, S.P., Robson, S.K. and Schwarzkopf, L., 2019. Ecological associations among epidermal microstructure and scale characteristics of Australian geckos (Squamata: Carphodactylidae and Diplodactylidae). *Journal of Anatomy*, *234*(6), pp.853-874.
Rhacodactylus auriculatus	Bauer, A.M., 1998. Morphology of the adhesive tail tips of carphodactyline geckos (Reptilia: Diplodactylidae). *Journal of Morphology*, *235*(1), pp.41-58.
Rhoptropus barnardi	Johnson, M.K. and Russell, A.P., 2009. Configuration of the setal fields of Rhoptropus (Gekkota: Gekkonidae): functional, evolutionary, ecological and phylogenetic implications of observed pattern. *Journal of Anatomy*, *214*(6), pp.937-955.
Rhoptropus boultoni	Johnson, M.K. and Russell, A.P., 2009. Configuration of the setal fields of Rhoptropus (Gekkota: Gekkonidae): functional, evolutionary, ecological and phylogenetic implications of observed pattern. *Journal of Anatomy*, *214*(6), pp.937-955.
Rhynchoedura ormsbyi	Riedel, J., Vucko, M.J., Blomberg, S.P., Robson, S.K. and Schwarzkopf, L., 2019. Ecological associations among epidermal microstructure and scale characteristics of Australian geckos (Squamata: Carphodactylidae and Diplodactylidae). *Journal of Anatomy*, *234*(6), pp.853-874.
Rhynchoedura ornata	Withers, P.C., Aplin, K.P. and Werner, Y.L., 2000. Metabolism and evaporative water loss of Western Australian geckos (Reptilia: Sauria: Gekkonomorpha). *Australian Journal of Zoology*, *48*(2), pp.111-126.
Salutarius cornutus	Riedel, J., Vucko, M.J., Blomberg, S.P., Robson, S.K. and Schwarzkopf, L., 2019. Ecological associations among epidermal microstructure and scale characteristics of Australian geckos (Squamata: Carphodactylidae and Diplodactylidae). *Journal of Anatomy*, *234*(6), pp.853-874.
Sphaerodactylus argus	Forys, E.A. and Allen, C.R., 1999. Biological invasions and deletions: community change in south Florida. *Biological Conservation*, *87*(3), pp.341-347.
Sphaerodactylus elegans	Forys, E.A. and Allen, C.R., 1999. Biological invasions and deletions: community change in south Florida. *Biological Conservation*, *87*(3), pp.341-347.
Strophurus ciliaris	Withers, P.C., Aplin, K.P. and Werner, Y.L., 2000. Metabolism and evaporative water loss of Western Australian geckos (Reptilia: Sauria: Gekkonomorpha). *Australian Journal of Zoology*, *48*(2), pp.111-126.

Strophurus krisalys	Riedel, J., Vucko, M.J., Blomberg, S.P., Robson, S.K. and Schwarzkopf, L., 2019. Ecological associations among epidermal microstructure and scale characteristics of Australian geckos (Squamata: Carphodactylidae and Diplodactylidae). *Journal of Anatomy*, *234*(6), pp.853-874.
Strophurus michaelseni	Withers, P.C., Aplin, K.P. and Werner, Y.L., 2000. Metabolism and evaporative water loss of Western Australian geckos (Reptilia: Sauria: Gekkonomorpha). *Australian Journal of Zoology*, *48*(2), pp.111-126.
Strophurus spinigerus	Withers, P.C., Aplin, K.P. and Werner, Y.L., 2000. Metabolism and evaporative water loss of Western Australian geckos (Reptilia: Sauria: Gekkonomorpha). *Australian Journal of Zoology*, *48*(2), pp.111-126.
Strophurus taeniatus	Riedel, J., Vucko, M.J., Blomberg, S.P., Robson, S.K. and Schwarzkopf, L., 2019. Ecological associations among epidermal microstructure and scale characteristics of Australian geckos (Squamata: Carphodactylidae and Diplodactylidae). *Journal of Anatomy*, *234*(6), pp.853-874.
Strophurus williamsi	Riedel, J., Vucko, M.J., Blomberg, S.P., Robson, S.K. and Schwarzkopf, L., 2019. Ecological associations among epidermal microstructure and scale characteristics of Australian geckos (Squamata: Carphodactylidae and Diplodactylidae). *Journal of Anatomy*, *234*(6), pp.853-874.

Table 2: Supplementary General and Microhabitat and location data collected for the species included in or added to, the main species list formed from the data in Meiri (2010) and Kulyomini *et al.* (2019).

Species	**Reference**
Afrogecko porphyreus	Griffin, M. and INVENTORY, B., 2003. *Annotated checklist and provisional conservation status of Namibian reptiles*. Namibia Scientific Society.
Agamura persica	Khan, M.S., 1999. Herpetology of habitat types of Pakistan. *Pakistan Journal of Zoology*, *31*(3), pp.275-289.
Agamura persica	Safaei-Mahroo, B., Ghaffari, H., Fahimi, H., Broomand, S., Yazdanian, M., Najafi-Majd, E., Hosseinian Yousefkhani, S.S., Rezazadeh, E., Hosseinzadeh, M.S., Nasrabadi, R. and Rajabizadeh, M., 2015. The herpetofauna of Iran: checklist of taxonomy, distribution and conservation status. *Asian Herpetological Research*, *6*(4), pp.257-290.
Ailuronyx seychellensis	Hill, M.J., Vel, T.M., Holm, K.J., Parr, S.J. and Shah, N.J., 2002. Cousin. *Atoll Research Bulletin*.
Amalosia rhombifer	Cogger, H., 2014. *Reptiles and amphibians of*

	Australia. Csiro Publishing, pp.290
Asaccus montanus	Gardner, A.S., 1994. A new species of Asaccus (Gekkonidae) from the mountains of northern Oman. *Journal of herpetology*, pp.141-145.
Bavayia cyclura	Bauer, A.M. and De Vaney, K.D., 1987. Comparative aspects of diet and habitat in some New Caledonian lizards. *Amphibia-Reptilia*, *8*(4), pp.349-364.
Blaesodactylus antongilensis	Evans, A., 2019. *The impact of habitat structure on reptile occurrence in a fragmented tropical landscape* (Doctoral dissertation).
Blaesodactylus antongilensis	Gehring, P.S., Ratsoavina, F.M. and Vences, M., 2010. Filling the gaps–amphibian and reptile records from lowland rainforests in eastern Madagascar. *Salamandra*, *46*(4), pp.214-234.
Blaesodactylus boivini	Jono, T., Bauer, A.M., Brennan, I. and Mori, A., 2015. New species of Blaesodactylus (Squamata: Gekkonidae) from Tsingy karstic outcrops in Ankarana National Park, northern Madagascar. *Zootaxa*, *3980*(3), pp.406-416.
Blaesodactylus boivini	D'Cruze, N. and Kumar, S., 2011. Effects of anthropogenic activities on lizard communities in northern Madagascar. *Animal Conservation*, *14*(5), pp.542-552.
Bunopus blanfordii	WERNER, Y.L., 1988. Herpetofaunal survey of Israel (1950-85), with comments on Sinai and Jordan and on zoogeographical heterogeneity. *Monographiae biologicae*, *62*, pp.355-388.
Bunopus tuberculatus	Cox, N.A., Mallon, D., Bowles, P., Els, J. and Tognelli, M.F., 2012. The Conservation Status and Distribution of Reptiles of the Arabian Peninsula. *Cambridge, UK and Gland, Switzerland: IUCN, and Sharjah, UAE: Environment and Protected Areas Authority*.
Bunopus tuberculatus	Khan, M.S., 1999. Herpetology of habitat types of Pakistan. *Pakistan Journal of Zoology*, *31*(3), pp.275-289.
Bunopus tuberculatus	Fathnia, B., RASTEGAR, P.N., Sampour, M., Bahrami, A.M. and Jaafari, G., 2009. The lizard fauna of Ilam province, Southwestern Iran.
Bunopus tuberculatus	Safaei-Mahroo, B., Ghaffari, H., Fahimi, H., Broomand, S., Yazdanian, M., Najafi-Majd, E., Hosseinian Yousefkhani, S.S., Rezazadeh, E., Hosseinzadeh, M.S., Nasrabadi, R. and Rajabizadeh, M., 2015. The herpetofauna of Iran: checklist of taxonomy, distribution and conservation status. *Asian Herpetological Research*, *6*(4), pp.257-290.
Calodactylodes illingworthorum	Karunarathna, D.M.S.S. and Amarasinghe, A.T., 2011. Natural history and conservation status of Calodactylodes illingworthorum Deraniyagala, 1953 (Sauria: Gekkonidae) in south-eastern Sri Lanka. *Herpetotropicos*, *6*(1-2), pp.5-10.
Carphodactylus laevis	Cogger, H., 2014. *Reptiles and amphibians of*

	Australia. Csiro Publishing, pp.262
Chatogekko amazonicus	Gamble, T., Daza, J.D., Colli, G.R., Vitt, L.J. and Bauer, A.M., 2011. A new genus of miniaturized and pug-nosed gecko from South America (Sphaerodactylidae: Gekkota). *Zoological journal of the Linnean Society*, *163*(4), pp.1244-1266.
Chondrodactylus angulifer	Pianka, E.R. and Huey, R.B., 1978. Comparative ecology, resource utilization and niche segregation among gekkonid lizards in the southern Kalahari. *Copeia*, pp.691-701.
Chondrodactylus angulifer	Griffin, M. and INVENTORY, B., 2003. *Annotated checklist and provisional conservation status of Namibian reptiles*. Namibia Scientific Society.
Chondrodactylus angulifer	Johnson, M.K., Russell, A.P. and Bauer, A.M., 2005. Locomotor morphometry of the Pachydactylus radiation of lizards (Gekkota: Gekkonidae): a phylogenetically and ecologically informed analysis. *Canadian Journal of Zoology*, *83*(12), pp.1511-1524.
Chondrodactylus bibronii	Johnson, M.K., Russell, A.P. and Bauer, A.M., 2005. Locomotor morphometry of the Pachydactylus radiation of lizards (Gekkota: Gekkonidae): a phylogenetically and ecologically informed analysis. *Canadian Journal of Zoology*, *83*(12), pp.1511-1524.
Chondrodactylus turneri	Johnson, M.K., Russell, A.P. and Bauer, A.M., 2005. Locomotor morphometry of the Pachydactylus radiation of lizards (Gekkota: Gekkonidae): a phylogenetically and ecologically informed analysis. *Canadian Journal of Zoology*, *83*(12), pp.1511-1524.
Chondrodactylus turneri	Hedman, H.D., Chuga, S.C., Eifler, D.A., Hanghome, G.P. and Eifler, M.A., 2021. Microhabitat use of two sympatric geckos, Turner's thick-toed gecko (Chondrodactylus turneri) and the Common Namib Day Gecko (Rhoptropus afer). *Journal of Arid Environments*, *188*, p.104448.
Christinus guentheri	Cogger, H., 2014. *Reptiles and amphibians of Australia*. Csiro Publishing, pp.347
Christinus marmoratus	Cogger, H., 2014. *Reptiles and amphibians of Australia*. Csiro Publishing, pp.348
Cnemaspis kandiana	Somaweera, R., 2009. Reproductive ecology of the Kandyan Day Gecko, Cnemaspis kandiana, in Gannoruwa Forest Reserve. *Journal of the National Science Foundation of Sri Lanka*, *37*(1).
Coleodactylus septentrionalis	Vitt, L.J., Sartorius, S.S., Avila-Pires, T.C.S., Zani, P.A. and Espósito, M.C., 2005. Small in a big world: ecology of leaf-litter geckos in new world tropical forests. *Herpetological monographs*, *19*(1), pp.137-152.
Coleonyx brevis	Riemer, W.J. ed., 1963. *Catalogue of American Amphibians and Reptiles* (No. 1-200).
Coleonyx brevis	Dial, B.E. and Grismer, L.L., 1992. A

	phylogenetic analysis of physiological-ecological character evolution in the lizard genus Coleonyx and its implications for historical biogeographic reconstruction. *Systematic Biology*, *41*(2), pp.178-195.
Coleonyx elegans	Dial, B.E., 1978. The thermal ecology of two sympatric, nocturnal Coleonyx (Lacertilia: Gekkonidae). *Herpetologica*, pp.194-201.
Coleonyx elegans	Dial, B.E. and Grismer, L.L., 1992. A phylogenetic analysis of physiological-ecological character evolution in the lizard genus Coleonyx and its implications for historical biogeographic reconstruction. *Systematic Biology*, *41*(2), pp.178-195.
Coleonyx mitratus	Riemer, W.J. ed., 1963. *Catalogue of American Amphibians and Reptiles* (No. 1-200).
Coleonyx mitratus	Dial, B.E. and Grismer, L.L., 1992. A phylogenetic analysis of physiological-ecological character evolution in the lizard genus Coleonyx and its implications for historical biogeographic reconstruction. *Systematic Biology*, *41*(2), pp.178-195.
Coleonyx reticulatus	Dial, B.E., 1978. The thermal ecology of two sympatric, nocturnal Coleonyx (Lacertilia: Gekkonidae). *Herpetologica*, pp.194-201.
Coleonyx reticulatus	Dial, B.E. and Grismer, L.L., 1992. A phylogenetic analysis of physiological-ecological character evolution in the lizard genus Coleonyx and its implications for historical biogeographic reconstruction. *Systematic Biology*, *41*(2), pp.178-195.
Coleonyx switaki	Dial, B.E. and Grismer, L.L., 1992. A phylogenetic analysis of physiological-ecological character evolution in the lizard genus Coleonyx and its implications for historical biogeographic reconstruction. *Systematic Biology*, *41*(2), pp.178-195.
Coleonyx variegatus	Hollenbeck, E., Hollingsworth, B.D. and Stepek, M.A., 2010. Herpetological Assessment for the Freeman Properties California State Parks and Recreation in Imperial County Contract C0754013 Final Report.
Coleonyx variegatus	Dial, B.E. and Grismer, L.L., 1992. A phylogenetic analysis of physiological-ecological character evolution in the lizard genus Coleonyx and its implications for historical biogeographic reconstruction. *Systematic Biology*, *41*(2), pp.178-195.
Colopus wahlbergii	Griffin, M. and INVENTORY, B., 2003. *Annotated checklist and provisional conservation status of Namibian reptiles*.

	Namibia Scientific Society.
Crenadactylus ocellatus	Cogger, H., 2014. *Reptiles and amphibians of Australia*. Csiro Publishing, pp.291
Cyrtodactylus cryptus	Loos, J., Wehrden, H.V., Dang, K.N. and Ziegler, T., 2012. Niche segregation in microhabitat use of three sympatric Cyrtodactylus in the Phong Nha-Ke Bang National Park, central Vietnam. *Herpetological Conservation and Biology*, *7*(1), pp.101-108.
Cyrtodactylus lateralis	Harvey, M.B., O'Connell, K.A., Wostl, E., Riyanto, A., Kurniawan, N., Smith, E.N. and Grismer, L.L., 2016. Redescription Cyrtodactylus lateralis (Werner)(Squamata: Gekkonidae) and phylogeny of the prehensile-tailed Cyrtodactylus. *Zootaxa*, *4107*(4), pp.517-540.
Cyrtopodion longipes	Tuniyev, B., Atayev, C. and Shammakov, S., 1998. Report on fauna of amphibians and reptiles from Eastern Kopet Dag in Turkmenistan. *Russian Journal of Herpetology*, *5*(1), pp.74-81.
Cyrtopodion scabrum	Cox, N.A., Mallon, D., Bowles, P., Els, J. and Tognelli, M.F., 2012. The Conservation Status and Distribution of Reptiles of the Arabian Peninsula. *Cambridge, UK and Gland, Switzerland: IUCN, and Sharjah, UAE: Environment and Protected Areas Authority*.
Cyrtopodion scabrum	Khan, M.S., 1999. Herpetology of habitat types of Pakistan. *Pakistan Journal of Zoology*, *31*(3), pp.275-289.
Cyrtopodion scabrum	Fathnia, B., RASTEGAR, P.N., Sampour, M., Bahrami, A.M. and Jaafari, G., 2009. The lizard fauna of Ilam province, Southwestern Iran.
Cyrtopodion scabrum	Safaei-Mahroo, B., Ghaffari, H., Fahimi, H., Broomand, S., Yazdanian, M., Najafi-Majd, E., Hosseinian Yousefkhani, S.S., Rezazadeh, E., Hosseinzadeh, M.S., Nasrabadi, R. and Rajabizadeh, M., 2015. The herpetofauna of Iran: checklist of taxonomy, distribution and conservation status. *Asian Herpetological Research*, *6*(4), pp.257-290.
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Lucasium steindachneri	Cogger, H., 2014. *Reptiles and amphibians of Australia*. Csiro Publishing, pp.314
Lucasium stenodactylum	Cogger, H., 2014. *Reptiles and amphibians of Australia*. Csiro Publishing, pp.314
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Lygodactylus tuberosus	Ramanamanjato, J.B., 2007. Reptile and amphibian communities along the humidity gradient and fragmentation effects in the littoral forests of southeastern Madagascar. *Biodiversity, Ecology and Conservation of Littoral Ecosystems in Southeastern Madagascar, Tolagnaro (Fort Dauphin). SI/MAB Series. Washington DC, USA: Smithsonian Institution*, pp.167-79.
Lygodactylus tuberosus	Theisinger, O. and Ratianarivo, M.C., 2015. Patterns of reptile diversity loss in response to degradation in the spiny forest of southern Madagascar. *Herpetological Conservation and Biology*, *10*(1), pp.273-283.
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Mediodactylus kotschyi orientalis	Schwarz, R., Gavriilidi, I.A., Itescu, Y., Jamison, S., Sagonas, K., Meiri, S. and Pafilis, P., 2016. Mediodactylus kotschyi in the Peloponnese peninsula, Greece: distribution and habitat. *Acta Herpetologica*, *11*(2), pp.179-187.
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Nephrurus stellatus	Cogger, H., 2014. *Reptiles and amphibians of Australia*. Csiro Publishing, pp.268
Nephrurus vertebralis	Cogger, H., 2014. *Reptiles and amphibians of Australia*. Csiro Publishing, pp.268
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Oedura coggeri	Cogger, H., 2014. *Reptiles and amphibians of Australia*. Csiro Publishing, pp.319
Oedura jowalbinna	Cogger, H., 2014. *Reptiles and amphibians of Australia*. Csiro Publishing, pp.321
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Pachydactylus bicolor	Johnson, M.K., Russell, A.P. and Bauer, A.M., 2005. Locomotor morphometry of the Pachydactylus radiation of lizards (Gekkota: Gekkonidae): a phylogenetically and ecologically informed analysis. *Canadian Journal of Zoology*, *83*(12), pp.1511-1524.
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Phelsuma laticauda	Gehring, P.S., Ratsoavina, F.M. and Vences, M., 2010. Filling the gaps–amphibian and reptile records from lowland rainforests in

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Phelsuma lineata	Raselimanana, A. P. 2010. The amphibians and reptiles of the Ambatovy-Analamay region. In Biodiversity, exploration, and conservation of the natural habitats associated with the Ambatovy project, eds. S. M. Goodman & V. Mass. Malagasy Nature, 3: 99-123.
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Phyllopezus pollicaris	Righi, A.F., Nascimento, L.B. and Galdino, C.A., 2012. Seasonal reproduction in the Rock Gecko Phyllopezus pollicaris from a rock field habitat in Southeastern Brazil. *Journal of Herpetology*, *46*(4), pp.632-636.
Phyllurus amnicola	Cogger, H., 2014. *Reptiles and amphibians of Australia*. Csiro Publishing, pp.272
Phyllurus championae	Cogger, H., 2014. *Reptiles and amphibians of Australia*. Csiro Publishing, pp.273
Phyllurus nepthys	Cogger, H., 2014. *Reptiles and amphibians of Australia*. Csiro Publishing, pp.275
Phyllurus ossa	Cogger, H., 2014. *Reptiles and amphibians of Australia*. Csiro Publishing, pp.276
Pseudogonatodes guianensis	Beirne, C., Burdekin, O. and Whitworth, A., 2013. Herpetofaunal responses to anthropogenic habitat change within a small forest reserve in Eastern Ecuador. *The Herpetological Journal*, *23*(4), pp.209-209.
Pseudogonatodes guianensis	Cole, C.J. and Kok, P.J., 2006. A new species of gekkonid lizard (Sphaerodactylinae: Gonatodes) from Guyana, South America. *American Museum Novitates*, *2006*(3524), pp.1-13.
Pseudogonatodes guianensis	Vitt, L.J., Sartorius, S.S., Avila-Pires, T.C.S., Zani, P.A. and Espósito, M.C., 2005. Small in a big world: ecology of leaf-litter geckos in new world tropical forests. *Herpetological monographs*, *19*(1), pp.137-152.
Pseudothecadactylus australis	Cogger, H., 2014. *Reptiles and amphibians of Australia*. Csiro Publishing, pp.325
Ptenopus garrulus maculatus	Bauer, A.M., 1995. HERPETOFAUNA OF THE LITTLE KAROO, WESTERN CAPE, SOUTH AFRICA WITH NOTES. *Herpetological Natural History*, *3*(1), pp.47-89.
Ptenopus garrulus maculatus	Pianka, E.R. and Huey, R.B., 1978. Comparative ecology, resource utilization and niche segregation among gekkonid lizards in the southern Kalahari. *Copeia*, pp.691-701.
Ptenopus garrulus maculatus	Griffin, M. and INVENTORY, B., 2003. *Annotated checklist and provisional conservation status of Namibian reptiles*. Namibia Scientific Society.
Ptychozoon lionatum	Grape, V.H., Turreira-Garcia, N., Holger-Schmidt, L., Chhang, P. and Srisanga, P., 2016. Postpartum phytomedicine and its. *Cambodian Journal of Natural History*, p.119.
Ptyodactylus hasselquistii	WERNER, Y.L., 1988. Herpetofaunal survey of Israel (1950-85), with comments on Sinai and Jordan and on zoogeographical heterogeneity. *Monographiae biologicae*, *62*, pp.355-388.
Rhacodactylus auriculatus	Bauer, A.M. and De Vaney, K.D., 1987.

	Comparative aspects of diet and habitat in some New Caledonian lizards. *Amphibia-Reptilia*, *8*(4), pp.349-364.
Rhoptropus barnardi	Griffin, M. and INVENTORY, B., 2003. *Annotated checklist and provisional conservation status of Namibian reptiles*. Namibia Scientific Society.
Rhoptropus barnardi	Johnson, M.K., Russell, A.P. and Bauer, A.M., 2005. Locomotor morphometry of the Pachydactylus radiation of lizards (Gekkota: Gekkonidae): a phylogenetically and ecologically informed analysis. *Canadian Journal of Zoology*, *83*(12), pp.1511-1524.
Rhoptropus boultoni	Griffin, M. and INVENTORY, B., 2003. *Annotated checklist and provisional conservation status of Namibian reptiles*. Namibia Scientific Society.
Rhoptropus boultoni	Johnson, M.K., Russell, A.P. and Bauer, A.M., 2005. Locomotor morphometry of the Pachydactylus radiation of lizards (Gekkota: Gekkonidae): a phylogenetically and ecologically informed analysis. *Canadian Journal of Zoology*, *83*(12), pp.1511-1524.
Rhynchoedura ormsbyi	Cogger, H., 2014. *Reptiles and amphibians of Australia*. Csiro Publishing, pp.330
Rhynchoedura ornata	Cogger, H., 2014. *Reptiles and amphibians of Australia*. Csiro Publishing, pp.330
Saltuarius corntus	Cogger, H., 2014. *Reptiles and amphibians of Australia*. Csiro Publishing, pp.278
Sphaerodacylus argivus	Brunt, M.A. and Davies, J.E. eds., 2012. *The Cayman Islands: natural history and biogeography* (Vol. 71). Springer Science & Business Media, pp.424.
Sphaerodactylus argus	Krysko, K.L. and Coleman, M., 2005. Ecological status of the Ocellated Gecko, Sphaerodactylus argus argus Gosse 1850, in Florida, with additional herpetological notes from the Florida Keys. *Caribbean Journal of Science*, *41*(1), pp.169-172.
Sphaerodactylus ariasae	Hedges, S.B. and Thomas, R., 2001. At the lower size limit in amniote vertebrates: a new diminutive lizard from the West Indies. *Caribbean journal of Science*, *37*(3/4), pp.168-173.
Sphaerodactylus caicosensis	Hailey, A., Wilson, B. and Horrocks, J. eds., 2011. *Conservation of Caribbean Island Herpetofaunas Volume 2: Regional Accounts of the West Indies*. Brill.
Sphaerodactylus cinereus	Dunson, W.A. and Bramham, C.R., 1981. Evaporative water loss and oxygen consumption of three small lizards from the Florida Keys: Sphaerodactylus cinereus, S. notatus, and Anolis sagrei. *Physiological Zoology*, *54*(2), pp.253-259.
Sphaerodactylus copei	Thomas, R., 1968. Notes on Antillean geckos (Sphaerodactylus). *Herpetologica*, *24*(1), pp.46-60.

Sphaerodactylus elegans	Fong, A., L. M. Diaz, and N. Viña 2005. Amphibians and reptiles. In Fong, A., D. Maceira F., W. S. Alverson, and t. Wachter (eds.), Cuba: Parcque Nacional Alejandro de Humboldt. Rapid Biological Inventories Report 14. The Field Museum, Chicago.
Sphaerodactylus glaucus	Cid-Mora, O. and Vásquez-Cruz, V., 2020. Notes on the distribution of the Central American Collared Geckolet, Sphaerodactylus glaucus (Squamata: Sphaerodactylidae), in Quintana Roo, Mexico. *Reptiles & Amphibians*, *27*(1), pp.56-57.
Sphaerodactylus klauberi	Daza, J.D., Pinto, B.J., Thomas, R., Herrera-Martinez, A., Scantlebury, D.P., GARCÍA, L.F., Balaraman, R.P., Perry, G. and Gamble, T., 2019. The sprightly little sphaerodactyl: Systematics and biogeography of the Puerto Rican dwarf geckos Sphaerodactylus (Gekkota, Sphaerodactylidae). *Zootaxa*, *4712*(2).
Sphaerodactylus klauberi	N.A. 2006. IGUANA CONSERVATION, NATURAL HISTORY, AND HUSBANDRY OF REPTILES. *IGUANA, 13*(1).
Sphaerodactylus macrolepis	Daza, J.D., Pinto, B.J., Thomas, R., Herrera-Martinez, A., Scantlebury, D.P., GARCÍA, L.F., Balaraman, R.P., Perry, G. and Gamble, T., 2019. The sprightly little sphaerodactyl: Systematics and biogeography of the Puerto Rican dwarf geckos Sphaerodactylus (Gekkota, Sphaerodactylidae). *Zootaxa*, *4712*(2).
Sphaerodactylus macrolepis	Lameiro, A.M.D., 2011. *Mitochondrial phylogeny of Sphaerodactylus species endemic to islands in the Mona Passage and its biogeographical implications* (Doctoral dissertation, University of Puerto Rico, Mayaguez (Puerto Rico)).
Sphaerodactylus macrolepis	Boal, C.W., 2008. Predation of a dwarf gecko (Sphaerodactylus macrolepis) by a Bridled Quail-dove (Geotrygon mystacea). *Journal of Caribbean Ornithology*, *21*(1), pp.50-51.
Sphaerodactylus molei	Auguste, R.J., Charles, S.P. and Murphy, J.C., 2015. An Updated Checklist of the Amphibians and Reptiles of the Aripo Savannas. *Living World, Journal of the Trinidad and Tobago Field Naturalists' Club*.
Sphaerodactylus molei	Charles, S.P. and Smith, S., 2008. Observations of reptiles on Huevos Island, Trinidad, with five lizard species newly recorded for the island. *Living World, Journal of the Trinidad and Tobago Field Naturalists' Club*.
Sphaerodactylus monensis	Lameiro, A.M.D., 2011. *Mitochondrial phylogeny of Sphaerodactylus species endemic to islands in the Mona Passage and its biogeographical implications* (Doctoral dissertation, University of Puerto Rico, Mayaguez (Puerto Rico)).
Sphaerodactylus nicholsi	López-Ortiz, R. and Lewis, A.R., 2004. Habitat selection by Sphaerodactylus nicholsi

	(Squamata: Gekkonidae) in Cabo Rojo, Puerto Rico. *Herpetologica*, *60*(4), pp.438-444.
Sphaerodactylus nicholsi	Daza, J.D., Pinto, B.J., Thomas, R., Herrera-Martinez, A., Scantlebury, D.P., GARCÍA, L.F., Balaraman, R.P., Perry, G. and Gamble, T., 2019. The sprightly little sphaerodactyl: Systematics and biogeography of the Puerto Rican dwarf geckos Sphaerodactylus (Gekkota, Sphaerodactylidae). *Zootaxa*, *4712*(2).
Sphaerodactylus nicholsi	N.A. 2006. IGUANA CONSERVATION, NATURAL HISTORY, AND HUSBANDRY OF REPTILES. *IGUANA, 13*(1).
Sphaerodactylus nigropunctatus	Dodd Jr, C.K., 2003. Turquoise water, silver palms and fluorescent green Leiocephalus.
Sphaerodactylus notatus	Fong, A., L. M. Diaz, and N. Viña 2005. Amphibians and reptiles. In Fong, A., D. Maceira F., W. S. Alverson, and t. Wachter (eds.), Cuba: Parcque Nacional Alejandro de Humboldt. Rapid Biological Inventories Report 14. The Field Museum, Chicago.
Sphaerodactylus notatus	Dunson, W.A. and Bramham, C.R., 1981. Evaporative water loss and oxygen consumption of three small lizards from the Florida Keys: Sphaerodactylus cinereus, S. notatus, and Anolis sagrei. *Physiological Zoology*, *54*(2), pp.253-259.
Sphaerodactylus notatus	Dodd Jr, C.K., 2003. Turquoise water, silver palms and fluorescent green Leiocephalus.
Sphaerodactylus parthenopion	MacLean, W.P., 1985. Water-loss rates of Sphaerodactylus parthenopion (Reptilia: Gekkonidae), the smallest amniote vertebrate. *Comparative Biochemistry and Physiology Part A: Physiology*, *82*(4), pp.759-761.
Sphaerodactylus torrei	Lemm, J. and Alberts, A. "Herps of Guantanamo Bay, Cuba."
Stenodactylus doriae	Cox, N.A., Mallon, D., Bowles, P., Els, J. and Tognelli, M.F., 2012. The Conservation Status and Distribution of Reptiles of the Arabian Peninsula. *Cambridge, UK and Gland, Switzerland: IUCN, and Sharjah, UAE: Environment and Protected Areas Authority*.
Stenodactylus doriae	WERNER, Y.L., 1988. Herpetofaunal survey of Israel (1950-85), with comments on Sinai and Jordan and on zoogeographical heterogeneity. *Monographiae biologicae*, *62*, pp.355-388.
Stenodactylus doriae	Zaady, E. and Bouskila, A., 2002. Lizard burrows association with successional stages of biological soil crusts in an arid sandy region. *Journal of arid environments*, *50*(2), pp.235-246.
Stenodactylus doriae	Safaei-Mahroo, B., Ghaffari, H., Fahimi, H., Broomand, S., Yazdanian, M., Najafi-Majd, E., Hosseinian Yousefkhani, S.S., Rezazadeh, E., Hosseinzadeh, M.S., Nasrabadi, R. and Rajabizadeh, M., 2015. The herpetofauna of

	Iran: checklist of taxonomy, distribution and conservation status. *Asian Herpetological Research*, *6*(4), pp.257-290.
Stenodactylus petrii	WERNER, Y.L., 1988. Herpetofaunal survey of Israel (1950-85), with comments on Sinai and Jordan and on zoogeographical heterogeneity. *Monographiae biologicae*, *62*, pp.355-388.
Stenodactylus sthenodactylus	WERNER, Y.L., 1988. Herpetofaunal survey of Israel (1950-85), with comments on Sinai and Jordan and on zoogeographical heterogeneity. *Monographiae biologicae*, *62*, pp.355-388.
Stenodactylus sthenodactylus	Spawls, S. and Rotich, D., 1997. An annotated checklist of the lizards of Kenya. *Journal of East African Natural History*, *86*(1), pp.61-83.
Strophurus ciliaris	Cogger, H., 2014. *Reptiles and amphibians of Australia*. Csiro Publishing, pp.334
Strophurus elderi	Cogger, H., 2014. *Reptiles and amphibians of Australia*. Csiro Publishing, pp.335
Strophurus intermedius	Cogger, H., 2014. *Reptiles and amphibians of Australia*. Csiro Publishing, pp.336
Strophurus krisalys	Cogger, H., 2014. *Reptiles and amphibians of Australia*. Csiro Publishing, pp.337
Strophurus michaelseni	Cogger, H., 2014. *Reptiles and amphibians of Australia*. Csiro Publishing, pp.338
Strophurus spinigerus	Cogger, H., 2014. *Reptiles and amphibians of Australia*. Csiro Publishing, pp.340
Strophurus strophurus	Cogger, H., 2014. *Reptiles and amphibians of Australia*. Csiro Publishing, pp.341
Strophurus taeniatus	Cogger, H., 2014. *Reptiles and amphibians of Australia*. Csiro Publishing, pp.341
Strophurus williamsi	Cogger, H., 2014. *Reptiles and amphibians of Australia*. Csiro Publishing, pp.343
Tarentola americana	Fong, A., L. M. Diaz, and N. Viña 2005. Amphibians and reptiles. In Fong, A., D. Maceira F., W. S. Alverson, and t. Wachter (eds.), Cuba: Parcque Nacional Alejandro de Humboldt. Rapid Biological Inventories Report 14. The Field Museum, Chicago.
Tarentola americana	Lemm, J. and Alberts, A. "Herps of Guantanamo Bay, Cuba."
Tarentola americana	Weiss, A.J. and Hedges, S.B., 2007. Molecular phylogeny and biogeography of the Antillean geckos Phyllodactylus wirshingi, Tarentola americana, and Hemidactylus haitianus (Reptilia, Squamata). *Molecular phylogenetics and evolution*, *45*(1), pp.409-416.
Tarentola americana	Dodd Jr, C.K., 2003. Turquoise water, silver palms and fluorescent green Leiocephalus.
Tarentola annularis	Johnson, M.K., Russell, A.P. and Bauer, A.M., 2005. Locomotor morphometry of the Pachydactylus radiation of lizards (Gekkota: Gekkonidae): a phylogenetically and ecologically informed analysis. *Canadian Journal of Zoology*, *83*(12), pp.1511-1524.
Tarentola crombiei	Alfonso, Y.U., Charruau, P., Fajardo, G. and

	Estrada, A.R., 2012. Interspecific communal oviposition and reproduction of three lizard species in Southeastern Cuba. *Herpetology Notes*, *5*, pp.73-77.
Tarentola mauritanica	Johnson, M.K., Russell, A.P. and Bauer, A.M., 2005. Locomotor morphometry of the Pachydactylus radiation of lizards (Gekkota: Gekkonidae): a phylogenetically and ecologically informed analysis. *Canadian Journal of Zoology*, *83*(12), pp.1511-1524.
Tenuidactylus caspius	Safaei-Mahroo, B., Ghaffari, H., Fahimi, H., Broomand, S., Yazdanian, M., Najafi-Majd, E., Hosseinian Yousefkhani, S.S., Rezazadeh, E., Hosseinzadeh, M.S., Nasrabadi, R. and Rajabizadeh, M., 2015. The herpetofauna of Iran: checklist of taxonomy, distribution and conservation status. *Asian Herpetological Research*, *6*(4), pp.257-290.
Teratoscincus microlepis	Khan, M.S., Habitat availability to amphibians and reptiles in Pakistan.
Teratoscincus microlepis	Khan, M.S., 1999. Herpetology of habitat types of Pakistan. *Pakistan Journal of Zoology*, *31*(3), pp.275-289.
Teratoscincus scincus	Khan, M.S., Habitat availability to amphibians and reptiles in Pakistan.
Thecadactylus rapicauda	Vitt, L.J. and Zani, P.A., 1997. Ecology of the nocturnal lizard Thecadactylus rapicauda (Sauria: Gekkonidae) in the Amazon region. *Herpetologica*, pp.165-179.
Thecadactylus rapicauda	Auguste, R.J., Charles, S.P. and Murphy, J.C., 2015. An Updated Checklist of the Amphibians and Reptiles of the Aripo Savannas. *Living World, Journal of the Trinidad and Tobago Field Naturalists' Club*.
Thecadactylus rapicauda	Cole, C.J. and Kok, P.J., 2006. A new species of gekkonid lizard (Sphaerodactylinae: Gonatodes) from Guyana, South America. *American Museum Novitates*, *2006*(3524), pp.1-13.
Thecadactylus rapicauda	Charles, S.P. and Smith, S., 2008. Observations of reptiles on Huevos Island, Trinidad, with five lizard species newly recorded for the island. *Living World, Journal of the Trinidad and Tobago Field Naturalists' Club*.
Tropiocolotes nattereri	Cox, N.A., Mallon, D., Bowles, P., Els, J. and Tognelli, M.F., 2012. The Conservation Status and Distribution of Reptiles of the Arabian Peninsula. *Cambridge, UK and Gland, Switzerland: IUCN, and Sharjah, UAE: Environment and Protected Areas Authority*.
Tropiocolotes nattereri	WERNER, Y.L., 1988. Herpetofaunal survey of Israel (1950-85), with comments on Sinai and Jordan and on zoogeographical heterogeneity. *Monographiae biologicae*, *62*, pp.355-388.
Tropiocolotes nattereri	Shifman, S., Shacham, B. and Werner, Y.L., 1999. Tropiocolotes nattereri (Reptilia: Gekkonidae): comments on validity, variation

	and distribution. *Zoology in the Middle East*, *17*(1), pp.51-66.
Tropiocolotes steudneri	WERNER, Y.L., 1988. Herpetofaunal survey of Israel (1950-85), with comments on Sinai and Jordan and on zoogeographical heterogeneity. *Monographiae biologicae*, *62*, pp.355-388.
Underwoodisaurus milii	Cogger, H., 2014. *Reptiles and amphibians of Australia*. Csiro Publishing, pp.283
Uroplatus ebenaui	Blumgart, D., Dolhem, J. and Raxworthy, C.J., 2017. Herpetological diversity across intact and modified habitats of Nosy Komba Island, Madagascar. *Journal of Natural History*, *51*(11-12), pp.625-642.
Uroplatus ebenaui	Raxworthy, C.J. and Nussbaum, R.A., 1994. A rainforest survey of amphibians, reptiles and small mammals at Montagne d'Ambre, Madagascar. *Biological conservation*, *69*(1), pp.65-73.
Uroplatus ebenaui	Evans, A., 2019. *The impact of habitat structure on reptile occurrence in a fragmented tropical landscape* (Doctoral dissertation).
Uroplatus ebenaui	Roberts, S.H. and Daly, C., 2014. A rapid herpetofaunal assessment of Nosy Komba Island, northwestern Madagascar, with new locality records for seventeen species. *Salamandra*, *50*(1), pp.18-26.
Uroplatus fimbriatus	Raxworthy, C.J. and Nussbaum, R.A., 1994. A rainforest survey of amphibians, reptiles and small mammals at Montagne d'Ambre, Madagascar. *Biological conservation*, *69*(1), pp.65-73.
Uroplatus fimbriatus	Gehring, P.S., Ratsoavina, F.M. and Vences, M., 2010. Filling the gaps–amphibian and reptile records from lowland rainforests in eastern Madagascar. *Salamandra*, *46*(4), pp.214-234.
Uroplatus guentheri	Evans, A., 2019. *The impact of habitat structure on reptile occurrence in a fragmented tropical landscape* (Doctoral dissertation).
Uroplatus henkeli	Blumgart, D., Dolhem, J. and Raxworthy, C.J., 2017. Herpetological diversity across intact and modified habitats of Nosy Komba Island, Madagascar. *Journal of Natural History*, *51*(11-12), pp.625-642.
Uroplatus henkeli	Evans, A., 2019. *The impact of habitat structure on reptile occurrence in a fragmented tropical landscape* (Doctoral dissertation).
Uroplatus henkeli	Roberts, S.H. and Daly, C., 2014. A rapid herpetofaunal assessment of Nosy Komba Island, northwestern Madagascar, with new locality records for seventeen species. *Salamandra*, *50*(1), pp.18-26.
Uroplatus lineatus	Gehring, P.S., Ratsoavina, F.M. and Vences, M., 2010. Filling the gaps–amphibian and reptile records from lowland rainforests in eastern Madagascar. *Salamandra*, *46*(4),

	pp.214-234.
Uroplatus phantasticus	Raselimanana, A. P. 2010. The amphibians and reptiles of the Ambatovy-Analamay region. In Biodiversity, exploration, and conservation of the natural habitats associated with the Ambatovy project, eds. S. M. Goodman & V. Mass. Malagasy Nature, 3: 99-123.
Uroplatus sikorae	Raselimanana, A. P. 2010. The amphibians and reptiles of the Ambatovy-Analamay region. In Biodiversity, exploration, and conservation of the natural habitats associated with the Ambatovy project, eds. S. M. Goodman & V. Mass. Malagasy Nature, 3: 99-123.
Uroplatus sikorae	D'Cruze, N. and Kumar, S., 2011. Effects of anthropogenic activities on lizard communities in northern Madagascar. *Animal Conservation*, *14*(5), pp.542-552.
Uroplatus sikorae	Ramanamanjato, J.B., 2007. Reptile and amphibian communities along the humidity gradient and fragmentation effects in the littoral forests of southeastern Madagascar. *Biodiversity, Ecology and Conservation of Littoral Ecosystems in Southeastern Madagascar, Tolagnaro (Fort Dauphin). SI/MAB Series. Washington DC, USA: Smithsonian Institution*, pp.167-79.
Uroplatus sikorae	Raxworthy, C.J. and Nussbaum, R.A., 1994. A rainforest survey of amphibians, reptiles and small mammals at Montagne d'Ambre, Madagascar. *Biological conservation*, *69*(1), pp.65-73.
Woodworthia maculatus	O'Donnell, C.F., Weston, K.A. and Monks, J.M., 2017. Impacts of introduced mammalian predators on New Zealand's alpine fauna. *New Zealand Journal of Ecology*, *41*(1), pp.1-22.

Table 3: Specimen location information for the toepad and claw images for some of the species analysed in this study, alongside whether they were living or preserved specimens.

Species	**Specimen Origin**	**Imaged Preserved or Live**	**Current Location**
Afrogecko porphyreus	South Africa	Preserved	American Museum of Natural History #147536
Agamura persica	Pakistan	Preserved	American Museum of Natural History #90427
Ailuronyx seychellensis	Seychelle Islands	Preserved	Museum of Comparative Zoology #R162913
Alsophylax pipiens	USSR, Kazaka SSR	Preserved	American Museum of Natural History #118983
Amalosia rhombifer	Queensland, Australia	Live	Queensland Museum #J92090
Bavayia cyclura	Noumea	Preserved	Museum of Comparative Zoology #R6209

Blaesodactylus antongilensis	Madagascar	Preserved	American Museum of Natural History #144141
Blaesodactylus boivini	Madagascar	Preserved	Museum of Comparative Zoology #R11629
Bunopus tuberculatus	Iraq	Preserved	Museum of Comparative Zoology #R56515
Carphodactylus laevis	Queensland, Australia	Preserved	Museum of Comparative Zoology #R35111
Chatogekko amazonicus	Brazil	Preserved	American Museum of Natural History #138699
Chondrodactylus angulifer	SW Africa	Preserved	American Museum of Natural History #116273
Chondrodactylus bibronii	SW Africa	Preserved	American Museum of Natural History #47866
Christinus marmoratus	No Data	Preserved	American Museum of Natural History #24941
Coleonyx brevis	Mexico	Preserved	American Museum of Natural History #155947
Coleonyx elegans	Mexico	Preserved	American Museum of Natural History #155955
Correlophus ciliatus	Captive Specimen	Live	Michigan State Univeristy
Crenadactylus ocellatus	Australia, North Terr.	Preserved	American Museum of Natural History #86326
Cyrtopodion scabrum	Pakistan	Preserved	American Museum of Natural History #85559
Tenuidactylus turcmenicus	USSR	Preserved	American Museum of Natural History #130552
Dactylocnemis pacificus	New Zealand	Preserved	California Academy of Sciences #47980
Diplodactylus conspicillatus	Australia	Preserved	American Museum of Natural History #99731
Diplodactylus tessellatus	Queensland, Australia	Live	Released
Ebenavia inunguis	Captive Specimen	Live	Boone private collection
Eublepharis macularius	Captive Specimen	Live	Mississippi University for Women
Garthia gaudichaudii	Chile	Preserved	American Museum of Natural History #38786
Geckolepis maculata	Madagascar	Preserved	Field Museum #18245
Gehyra mutilata	Oahu, Hawaii, USA	Live	Released
Gehyra oceanica	Palau, Koror State	Preserved	California Academy of Sciences #248962
Gehyra punctata	Australia: Northern Terr	Preserved	American Museum of Natural History #120285
Gehyra variegata	Queensland, Australia	Live	Queensland Museum #J92129
Gekko gekko	Captive Specimen	Live	Boone private collection
Gekko vittatus	Captive Specimen	Live	Akron University
Gonatodes albogularis	Nicaragua	Preserved	Carnegie Museum #67183
Gonatodes annularis	Brazil	Preserved	American Museum of Natural History #138715

Gonatodes antillensis	Bonaire, Carribean	Preserved	Carnegie Museum #47677
Gonatodes concinnatus	Ecuador	Preserved	American Museum of Natural History #57453
Gonatodes hasemani	Bolivia	Preserved	American Museum of Natural History #22542
Gonatodes humeralis	Peru	Preserved	American Museum of Natural History #56344
Gymnodactylus geckoides	Brazil	Preserved	American Museum of Natural History #131818
Hemidactylus brookii	Niger	Preserved	Field Museum #262272
Hemidactylus fasciatus	Nigeria	Preserved	American Museum of Natural History #103170
Hemidactylus flaviviridus	Afganistan	Preserved	Field Museum #161147
Hemidactylus frenatus	Oahu, Hawaii, USA	Live	Released
Hemidactylus garnotii	Vietnam	Preserved	American Museum of Natural History #147111
Hemidactylus leschenaultii	Sri Lanka	Preserved	American Museum of Natural History #96059
Hemidactylus mabouia	South Africa	Preserved	Field Museum #220206
Hemidactylus mercatorius	Malawi	Preserved	American Museum of Natural History #73184
Hemidactylus palaichthus	Guyana	Preserved	American Museum of Natural History #139751
Hemidactylus platyurus	Captive Specimen	Live	Boone private collection
Hemidactylus turcicus	Columbus, Mississippi, USA	Live	Mississippi University for Women
Hemitheconyx caudicinctus	Mali	Preserved	American Museum of Natural History #150678
Heteronotia binoei	Queensland, Australia	Live	Released
Holodactylus africanus	Kenya	Preserved	American Museum of Natural History #90627
Homonota darwinii	Argentina	Preserved	American Museum of Natural History #46430
Homopholis wahlbergii	South Africa	Preserved	American Museum of Natural History #18198
Hoplodactylus duvaucelii	Captive Specimen	Live	Kiwi Birdlife Park, New Zealand
Lepidoblepharis xanthostigma	Costa Rica	Preserved	Field Museum #177433
Lepidodactylus lugubris	Oahu, Hawaii, USA	Live	Released
Lucasium damaeus	Australia, South Australia	Preserved	American Museum of Natural History #86351
Lucasium immaculatum	Queensland, Australia	Live	Released
Lucasium steindachneri	Queensland, Australia	Live	Released

Lucasium stenodactylum	Queensland, Australia	Live	Released
Lygodactylus capensis	Tanzania	Preserved	American Museum of Natural History #142699
Lygodactylus chobiensis	Rhodesia	Preserved	American Museum of Natural History #114374
Lygodactylus gutturalis	Belgian Congo	Preserved	American Museum of Natural History #10308
Lygodactylus klugei	Brazil	Preserved	American Museum of Natural History #131821
Lygodactylus madagascariensis	Madagascar	Preserved	American Museum of Natural History #47831
Lygodactylus miops	Madagascar	Preserved	American Museum of Natural History #140236
Lygodactylus picturatus	Belgian Congo Kenya, Africa	Preserved	American Museum of Natural History #10343
Mediodactylus kotschyi orientalis	Israel	Preserved	American Museum of Natural History #68175
Mokopirirakau granulatus	Captive Specimen	Live	Kiwi Birdlife Park, New Zealand
Nactus pelagicus	Papua New Guinea	Preserved	American Museum of Natural History #99561
Nephrurus asper	Queensland, Australia	Live	Released
Nephrurus levis	Queensland, Australia	Live	Released
Oedura bella	Queensland, Australia	Live	Queensland Museum #J92095
Oedura castelnaui	Queensland, Australia	Live	James Cook University, Australia
Oedura cincta	Queensland, Australia	Live	Queensland Museum #J92118
Oedura coggeri	Queensland, Australia	Live	Queensland Museum #J92099
Oedura marmorata	Australia, Northern Territory	Preserved	American Museum of Natural History #86344
Oedura monilis	Queensland, Australia	Live	Queensland Museum #J92084
Oedura tryoni	Australia	Preserved	American Museum of Natural History #20865
Pachydactylus capensis	South Africa	Preserved	American Museum of Natural History #31611
Pachydactylus maculatus	South Africa	Preserved	American Museum of Natural History #8945
Pachydactylus mariquensis	South Africa	Preserved	American Museum of Natural History #18339
Pachydactylus punctatus	Angola	Preserved	American Museum of Natural History #47870
Paroedura bastardi	Madagascar	Preserved	American Museum of Natural History #71422
Paroedura gracilis	Madagascar	Preserved	American Museum of Natural History #144148
Phelsuma abbott	Aldabra	Preserved	Field Museum #18247
Phelsuma astriata	Seychelles	Preserved	American Museum of Natural History #90435
Phelsuma cepediana	Mauritius	Preserved	Field Museum #71678
Phelsuma dubia	No Data	Preserved	Field Museum #209460
Phelsuma grandis	Madagascar	Preserved	American Museum of Natural History

			#153154
Phelsuma guentheri	Seychelle	Preserved	American Museum of Natural History #24698
Phelsuma guttata	Madagascar	Preserved	American Museum of Natural History #144152
Phelsuma laticauda	Kauai, Hawaii	Live	Bernice Pauahi Bishop Museum
Phelsuma lineata	Madagascar	Preserved	American Museum of Natural History #71417
Phelsuma mutabilis	Madagascar	Preserved	American Museum of Natural History #47888
Phelsuma pusilla	Madagascar	Preserved	American Museum of Natural History #139144
Phelsuma sundbergi	Seychelles	Preserved	American Museum of Natural History #90443
Phyllodactylus kofordi	Peru	Preserved	American Museum of Natural History #28465
Phyllodactylus lanei	Mexico	Preserved	American Museum of Natural History #106350
Phyllodactylus microphyllus	Peru	Preserved	American Museum of Natural History #36514
Phyllodactylus reissii	Peru	Preserved	American Museum of Natural History #28426
Phyllodactylus unctus	Mexico	Preserved	American Museum of Natural History #97191
Phyllodactylus wirshingi	Captive Specimen	Live	Boone private collection
Phyllodactylus xanti	Baja California, Mexico	Preserved	American Museum of Natural History #77412
Phyllopezus pollicaris	Bolivia	Preserved	American Museum of Natural History #141635
Pseudothecadactylus australis	Queensland, Australia	Live	Queensland Museum #J92117
Ptenopus garrulus	SW Africa	Preserved	American Museum of Natural History #116284
Ptychozoon kuhli	No Data	Preserved	American Museum of Natural History #17
Ptyodactylus guttatus	Israel	Preserved	American Museum of Natural History #143585
Ptyodactylus hasselquistii	Ethiopia	Preserved	American Museum of Natural History #20052
Rhacodactylus auriculatus	Captive Specimen	Live	Akron University
Rhacodactylus leachianus	Loyalty Island	Preserved	American Museum of Natural History #62686
Rhoptropus barnardi	Southwest Africa: W. Kaokoland	Preserved	American Museum of Natural History #116288
Rhoptropus boultoni	Namibia	Preserved	Carnegie Museum #119457
Rhynchoedura ornata	Australia	Preserved	American Museum of Natural History #86348
Salutarius cornutus	Queensland, Australia	Preserved	American Museum of Natural History #120292
Sphaerodactylus	Jamaica	Preserved	American Museum of Natural History

argus			#145231
Sphaerodactylus caicosensis	Bahamas	Preserved	American Museum of Natural History #76137
Sphaerodactylus cinereus	Cuba	Preserved	American Museum of Natural History #78290
Sphaerodactylus copei	Haiti	Preserved	American Museum of Natural History #92801
Sphaerodactylus macrolepis	St. Croix, Virgin Islands	Preserved	American Museum of Natural History #145386
Sphaerodactylus nigropunctatus	Bahama Islands	Preserved	American Museum of Natural History #145362
Sphaerodactylus notatus	Cuba	Preserved	American Museum of Natural History #78348
Stenodactylus petrii	Israel	Preserved	American Museum of Natural History #143588
Stenodactylus sthenodactylus	Israel	Preserved	American Museum of Natural History #143586
Strophurus ciliaris	Queensland, Australia	Live	Queensland Museum #J92113
Strophurus elderi	Australia	Preserved	American Museum of Natural History #24928
Strophurus krisalys	Queensland, Australia	Live	Queensland Museum #J92104
Strophurus michaelseni	Australia	Preserved	American Museum of Natural History #86323
Strophurus spinigerus	Australia	Preserved	American Museum of Natural History #61068
Strophurus taeniatus	Queensland, Australia	Live	Released
Strophurus williamsi	Queensland, Australia	Live	James Cook University, Australia
Tarentola americana	Cuba	Preserved	American Museum of Natural History #81203
Tarentola annularis	Captive Specimen	Live	Akron University
Tarentola mauritanica	Spain	Preserved	American Museum of Natural History #94358
Tenuidactylus caspius	Turkmenistan	Preserved	California Academy of Sciences #184528
Tenuidactylus fedtschenkoi	USSR	Preserved	American Museum of Natural History #118987
Teratoscincus microlepis	West Pakistan	Preserved	American Museum of Natural History #96176
Teratoscincus scincus	West Pakistan	Preserved	American Museum of Natural History #88533
Thecadactylus rapicauda	Captive Specimen	Live	Boone private collection
Underwoodisaurus milii	Western Australia	Preserved	American Museum of Natural History #99781
Uroplatus ebenaui	Madagascar	Preserved	American Museum of Natural History #152939
Uroplatus fimbriatus	Madagascar	Preserved	American Museum of Natural History #152895
Uroplatus guentheri	Madagascar	Preserved	University of Michigan Museum of Zoology #217068
Uroplatus henkeli	Madagascar	Preserved	American Museum of Natural History #152904

Uroplatus lineatus	Madagascar	Preserved	American Museum of Natural History #159691
Uroplatus phantasticus	Madagascar	Preserved	University of Michigan Museum of Zoology #217099
Uroplatus sikorae	Madagascar	Preserved	American Museum of Natural History #152923
Woodworthia chrysosiretica	Captive Specimen	Live	Orana Wildlife Park, New Zealand
Woodworthia maculatus	Captive Specimen	Live	Orana Wildlife Park, New Zealand

Appendix 2

Non-Significant Results:

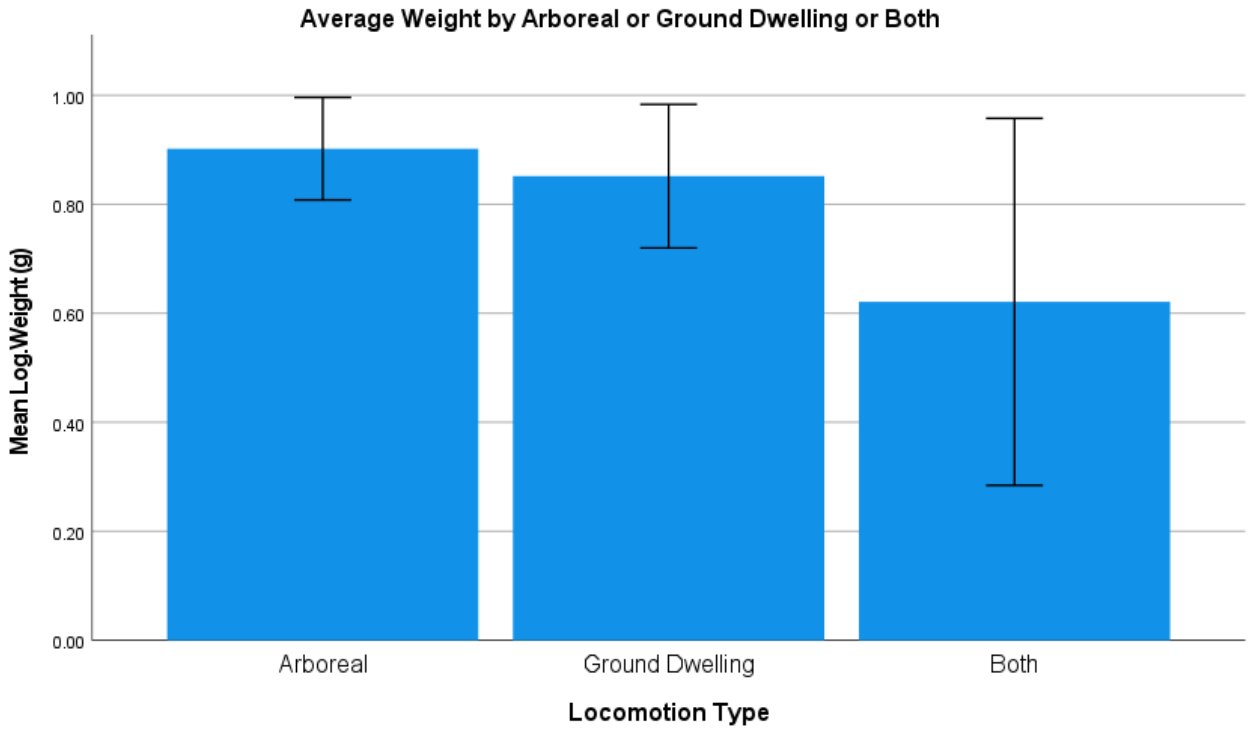

Figure 23: Mean logarithmically transformed weight of 151 species of gecko when grouped via their locomotion type (One-Way ANOVA, 2 df, p= 0.161). Geckos placed in the category 'Both' were those that could/did climb but only using their claws. They did not possess adhesive toepads.

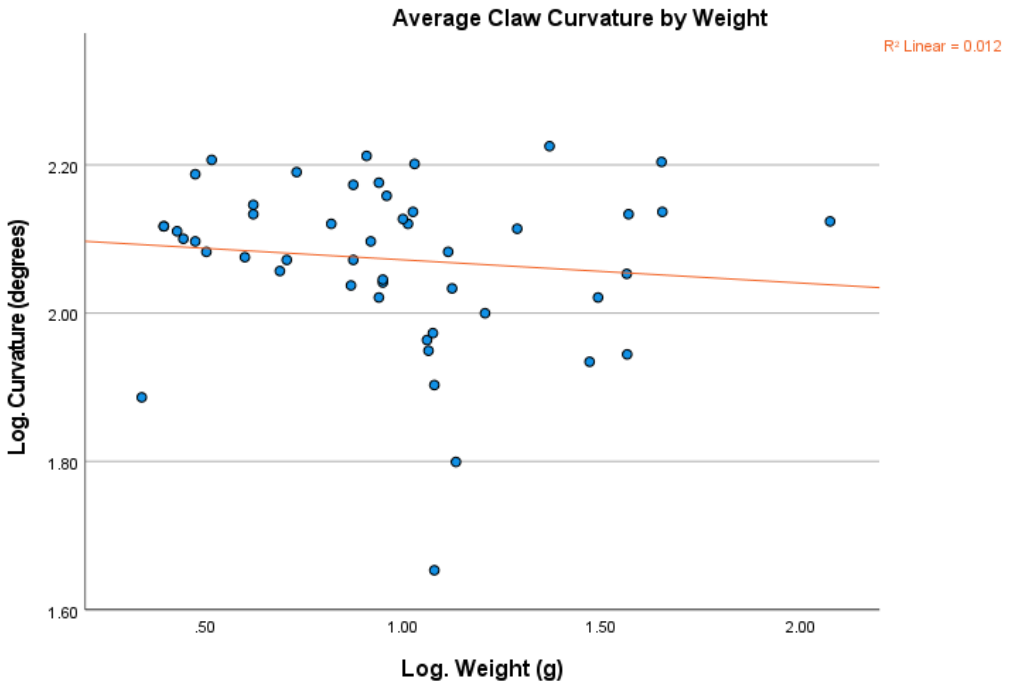

Figure 24: Linear regression of the logarithmically size corrected claw curvature and weight values for 49 species of gecko, showing that there is a weak relationship between claw curvature and body weight (r^2= 0.012), among these species of gecko.

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