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Qualifications:

Michael Yuan is a PhD candidate and Philomathia Fellow in the Wang Lab at the UC Berkeley, an affiliated graduate student at the Museum of Vertebrate Zoology (MVZ), and a Smithsonian Institution Predoctoral Fellow in the Bell Lab at the National Museum of Natural History (NMNH). He received his *B.S.* in both biological sciences and natural resources from Cornell University. He has over eight years of experience in biological research in both the lab and field primarily working in the Caribbean and Southeastern United States on a variety of amphibians and reptiles. He has previously worked in biological research for Archbold Biological Station and as lab manager at Duke University. His research primarily focuses on understanding adaptation to environmental stress in Caribbean anoles.

Jeffery Frederick is a PhD candidate and National Science Foundation Graduate Student Research Fellow in the McGuire Lab at UC Berkeley and the MVZ. He has over 13 years of experience in biological research and has contributed thousands of specimens to natural history collections. His work on wildlife ecology spans broad taxonomic disciplines (bats, seabirds, large mammals, reptiles, and amphibians). His current doctoral research under the curator of Herpetology at the UC Museum of Vertebrate Zoology focuses on the landscape ecology and adaptive evolution of amphibians in tropical island systems. He holds a *B.S.* in Biology from Christopher Newport University in Virginia, and an *M.S.* in Wildlife Biology and Conservation from the University of Alaska Fairbanks. Over his career, Jeff has worked as an agency biologist for the US Forest Service, US Geological Survey, Utah Division of Oil, Gas, and Mining, Nevada Department of Fish and Wildlife, and the Spatial Ecosystem Analysis Lab in Juneau, Alaska.

Research Proposal

Study #1: Evolution of *Anolis* in response to xeric-mesic gradients

Background: Repeated convergent evolution has captured the interest of generations of biologists in part because it implies some degree of determinism in evolution, whether through natural selection toward common adaptive peaks or shared evolutionary constraints (Losos 2011). Although phenotypic convergence is a widely occurring phenomenon, our understanding of the degree of overlap between phenotypic convergence and convergence in the underlying cellular, developmental, and genetic architecture is limited. On the genetic level, the prevailing hypothesis is that the more closely related the species or populations, the more likely that similar adaptive phenotypes are generated through the same genetic pathways due to selection acting on a more similar genetic background (Simpson 1967; Arendt and Reznick 2008; Conte et al. 2012). If this hypothesis is true, it is likely that convergence in developmental and cellular pathways that mediate the relationship between genotype and phenotype follow a similar pattern. However, recent work on the molecular basis of convergence has shown that although the expected pattern is sometimes observed (Colosimo et al. 2005; Wood et al. 2005), these general hypotheses may be unsupported for many groups (Hoekstra and Nachman 2003; Hoekstra et al. 2006; Rosenblum et al. 2010). Thus, the degree to which phenotypic convergence is mirrored by convergence in underlying genetic and cellular architecture at varying evolutionary scales remains unresolved. Here, we propose to leverage the striking phenotypic convergence across the Lesser Antillean anoles to examine the interplay of evolutionary scales and the overlap of genetic, cellular, and phenotypic patterns of convergence.

The Lesser Antilles were independently colonized by two divergent groups of *Anolis*. The Windward Islands were colonized by the *roquet* series from South America, whereas the Leeward Islands were colonized by the *bimaculatus* series from the Greater Antilles (Underwood 1959). Each island consists of one or two *Anolis* species, which display remarkable within-species phenotypic variation despite high levels of gene flow between populations (Stenson et al. 2002). The *roquet* series and at least two species in the *bimaculatus* series show strong phenotypic convergence in response to similar xeric-mesic environmental gradients across islands (Thorpe et al., 2015). Within each species, coastal xeric forms are paler in coloration, while montane mesic forms are brighter green/blue. These phenotypic patterns have also arisen independently multiple times within a species for several anoles (Thorpe et al. 2015). Thus, the Lesser Antillean anoles provide an opportunity to conduct comparative studies of adaptive color convergence at various phylogenetic scales (across populations, across closely-related species within a series, and across distantly-related clades).

Sint Maarten are home to two species of *Anolis* lizards: *A. gingivinus* and *A. pogus*. Both species exhibit dramatic variation in coloration and pattern throughout their range (Lazell 1972). Sint Maarten displays a range of habitats found throughout the Lesser Antilles including coastal dry scrub and interior mesic forest. However, variation in color and pattern as it relates to habitat differences has not been extensively examined in these

species. We propose to sample *A. gingivinus* and *A. pogus* to understand habitat adaptation in each species. This research will be part of a broader study encompassing multiple Lesser Antillean islands in order to study the mechanisms behind color evolution and adaptation to xeric-mesic habitat gradients in anoles.

Questions: (I) Are xeric and mesic populations of *A. gingivinus* and *A. pogus* different morphologically (i.e. color, scalation, skeletal structure) and ecologically (i.e. abundance, diet, perch behavior)? (III) What are the cellular and genetic underpinnings of these differences? (II) Are these differences consistent with differences observed in other species of *Anolis* in the Lesser Antilles?

Protocol: We propose to sample up to 50 individuals of each species (*A. pogus* and *A. gingivinus*). For each individual we will take field measurements including snout-vent length, perch height, and perch substrate. These individuals will be broadly surveyed in order to understand genetic structure and gene flow between xeric and mesic habitats. Animals surveyed for this purpose will be measured, photographed, and released alive at site of capture after removing 1-2cm of tail tissue for genetic analysis. Each individual will be acclimated in an opaque cloth bag to reduce stress following capture in order to better standardize color photographs before release. Lizards have innate ability to autotomize their tails (Cox 1969) allowing removal of a small amount of tissue for genetic analysis without substantially adversely impacting the animal (Langkilde and Shine 2006; García-Muñoz et al. 2011; Herrel et al. 2012).

For a subset of five male individuals of *A. gingivinus* from one dry site and one wet site. Each individual will be acclimated in an opaque cloth bag to reduce stress following capture. We will then photograph each individual and measure color using a portable spectrometer. Because liver and skin are primary pigment metabolizing organs, we will humanely euthanize these 10 individuals following protocols approved by the University of California Animal Use and Care Committee and collect relevant organs in RNA later for gene expression analyses. Additionally, a second in formaldehyde for histological study. Specimens will then be prepared as scientific research specimens for deposit in the Museum of Vertebrate Zoology as a resource for the broader scientific community. Additionally, euthanized *A. gingivinus* will be used for detailed morphological study including x-ray and CT-scanning analyses. We recognize that lethal sampling techniques may be undesirable and so are willing to forgo this aspect of the project or adjust sampling numbers at the discretion of the Nature Foundation Sint Maarten. Because *A. pogus* populations are vulnerable and of conservation concern, we are not requesting non-lethal sampling of the species.

Tissues will be shipped back to the United States for analyses. To place our study in the evolutionary context of *Anolis* on Sint Maarten, we will use DNA from both our focal population and additional georeferenced tail clips. We will sequence samples using restriction-site associated DNA sequencing (RAD-seq) to examine genetic population structure throughout the island and to model gene flow between xeric and mesic regions. Skin tissue will be examined using a combination of light and transmission electron (TEM) microscopy at the University of California, Berkeley's Electron Microscopy Lab.

We will examine the distribution and structure of color producing chromatophore cells within the epidermis of each lizard to understand how cellular morphology is related to coloration. Finally, we will sequence transcriptomes (RNA-seq) for skin tissue to examine differences in gene expression between xeric and mesic populations relating to habitat adaptation and coloration.

Preliminary Data: We have previously completed fieldwork studying *A. lividus* on the island of Montserrat as part of our broader study. We demonstrate clear morphological patterns in *A. lividus* which correlates with habitat and climatic (temperature and precipitation) differences across the island. For example, we demonstrate reserve Bergmann's rule or smaller individuals in cooler climates (ANOVA: $F = 7.90$, $P = 0.005$) as trend that has been observed in other reptiles (Ashton and Feldman 2007). We also show evidence of Allen's rule of shorter appendages relative to body size in cooler climates ($F = 7.90$, $P = 0.011$; Fig. 1A) similar to what has been described in other anoles (Jaffe et al. 2016). Montane rainforest populations of *A. lividus* also have fewer and larger scales compared to coastal xeric populations ($F = 9.23$, $P = 0.006$; Fig. 1B), as well as being darker and greener (all $R^2 > 0.368$, $P < 0.001$). These patterns of scalation and color demonstrate constituent patterns in response to habitat variation extends to *bimaculatus* series anoles in the Leeward Islands suggesting that broad comparative studies are possible in this system (Thorpe et al. 2015). We are continuing to process samples from Montserrat including cellular and genetic work described above (see Protocol). Additionally, we have recently completed field work on Sint Eustatius, Saint Kitts, and Nevis toward the proposed project. Our work on Montserrat provides a first case study in xeric-mesic adaptation in anoles from which we will build comparative studies following the completion of planned sampling on additional species and islands.

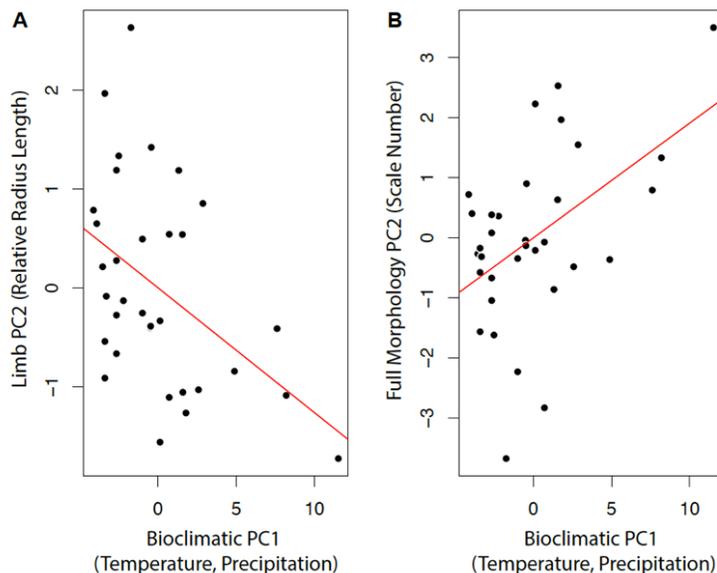


Fig. 1 For *A. lividus*: (A) Plot of limb PC2 and bioclimatic PC1 (temperature and precipitation) showing adherence to Allen's rule. (B) Plot of morphology PC2 (inverse scale number) and bioclimatic PC1. For A and B, dominant variables for each PC are denoted. Precipitation and temperature are inversely related.

Broader Impacts: These data will be used for non-commercial scientific research. Our primary goal is the dissemination of new knowledge. To that end, we will publish research findings in peer-reviewed scientific journals. Upon any publication, either scientific or popular press, we will provide PDF copies to the Nature Foundation Sint

Maarten. We welcome opportunities to collaborate with local scientists should there be interest, including authorship on any publications for which they substantially contribute. Additionally, we will provide all data files, field notes, and photographs to the Nature Foundation Sint Maarten for their use. This study will broadly contribute to our understanding of convergent evolution and adaptation to habitat gradients. We also hope to contribute information of value to the people of Sint Maarten including a systematic inventory of diversity within native anoles and estimates of genetic diversity which may be valuable for management planning particularly for the vulnerable *A. pogus*. Finally, this project will be used to construct outreach activities highlighting the diversity of the Lesser Antilles including exhibits at the Museum of Vertebrate Zoology, the California Academy of Sciences, and the National Museum of Natural History. The investigators have previously worked with or are affiliated with each of these institutions. Any public educational material produced from this research will also be provided to the Nature Foundation Sint Maarten for use.

Study #2: Comparative phylogeography of Leeward Island amphibians and reptiles

Background: The Leeward Islands of the Lesser Antilles form a volcanic island chain in the along the edge of the Caribbean plate (Tomblin 1975; Kopp et al. 2011). A global biodiversity hotspot (Myers et al. 2000), the Lesser Antilles are characterized by high rates of endemism across islands and colonization by both South American and Greater Antillean lineages. Despite the high levels of diversity and extensive work on geological history, population genetic and phylogeographic study of the region remains limited. Studies have generally focused on the history of colonization between islands (Kaiser 1997; Carstens et al. 2004; Stenson et al. 2004; Martin et al. 2015). Yet, distributions remain idiosyncratic and for many species our understanding both interisland colonization and how within island forces shapes genetic structure remain limited.

Our research focused on understanding the evolutionary history of the Lesser Antilles through comparative study of amphibians and reptiles. Specifically, we are focusing on three groups: *Eleutherodactylus johnstonei* (Antilles whistling frog), *Thecadactylus* geckos (turnip-tailed geckos), and *Sphaerodactylus* geckos (least geckos). Each of these are widely distributed throughout the Lesser Antilles, although their evolutionary histories are distinct. Thus, they provide an opportunity to examine the shared and divergent forces which has shaped their colonization of the Lesser Antilles and within island genetic diversity.

Eleutherodactylus johnstonei – Widespread throughout the Lesser Antilles, the native range of *E. johnstonei* is uncertain (Kaiser 1997). It is believed that they are native to the northern Lesser Antilles including Sint Maarten, however, three distinct origins have been suggested including a northern Lesser Antillean origin, a southern Lesser Antillean origin, and a Barbados origin (Kaiser 1997). *Eleutherodactylus johnstonei* is also one of the most widespread invasive species globally (Rödger 2010; Ernst et al. 2011). Therefore, *E. johnstonei* presents an opportunity to not only study the evolutionary history of widespread native species throughout the Lesser Antilles, but also to answer questions about its endemism. Using next-generation sequencing and demographic modeling, we will attempt to infer the origin of *E. johnstonei*, and the route of spread throughout the Lesser Antilles both natural and human-mediated.

Thecadactylus geckos – Turnip-tailed geckos (genus *Thecadactylus*) are a cosmopolitan species complex ranging from the Yucatan to the Amazon basin and the Lesser Antilles. Previous studies have shown that genetic diversity in mainland *Thecadactylus rapicauda* is limited throughout their range (Kronauer et al. 2005; Bergmann and Russell 2007). However, these studies were limited in data to a single gene and the recent description of new species in the Amazon headwaters (*T. solimoensis*) and Sint Maarten (*T. oskrobapreinatorum*) suggest that cryptic diversity exists within this species (Bergmann and Russell 2007; Koehler and Vesely 2011). Additionally, historical sampling in the Lesser Antilles is poor limiting the potential to understand phylogeographic history in the region. Therefore, we propose to utilize next-generation sequencing to examine fine-scale diversity of *T. rapicauda* and *T. oskrobapreinatorum* throughout the Lesser Antilles

including inferring routes of colonization from the mainland and subsequent spread across islands.

Sphaerodactylus geckos – Geckos within the genus *Sphaerodactylus* are widely distributed throughout the Americas including the Caribbean. We are interested in the evolutionary history of species which inhabit the islands of the Lesser Antilles. Sint Eustatius is home to two species: *S. parvus* and *S. sputator*. Both of these species are widely distributed in the northern Leeward islands. Much like their southern relatives, *S. vincenti* and *S. fantasticus* (Thorpe *et al.*, 2008; Surget-Groba & Thorpe, 2012), these nominal species likely form species complexes throughout these islands. We propose to examine the evolutionary history of *S. parvus* and *S. sputator* in the Leeward Islands in comparison with our other focal taxa to understand similarities and differences in routes of colonization and diversification after isolation. We will examine evidence for cryptic diversity and genetically distinct lineages within these species complexes throughout the Lesser Antilles.

Invasive species – In addition to our focal native species, we propose to collect tissues from invasive amphibians and reptiles. Invasive species may be important vectors of diseases which affect native species including Bd fungus in frogs and malaria in squamate reptiles. Although not a direct focus of our research, we collaborate with researchers interested in disease ecology and the spread of global invasive species. We will work with our collaborators to incorporate tissues collected from invasive species into our understanding of the role of invasive in disease dynamics throughout the Caribbean. Specifically, we propose to collect samples from three known invasives: the Cuban tree frog (*Osteopilus septentrionalis*), the red-snouted tree frog (*Scinax ruber*), and the house gecko (*Hemidactylus mabouia*).

Questions: (I) How are populations within a species related across the Lesser Antilles? (II) How is genetic diversity distributed across and within islands? (III) What is the colonization history and timing of each species throughout the Lesser Antilles and how does that relate to the volcanic history of the region? (IV) Are phylogeographic patterns, i.e. Questions I-III, consistent across species? (V) Is there cryptic diversity within species?

Protocol: Sampling will take place throughout Sint Maarten in order to fully sample the distribution of each study organism. We will sample a maximum of 25 individuals for *E. johnstonei* distributed across the island (Table 1). Frogs will be captured by hand. To characterize the distribution of dorsal patterns we will photograph each individual in a standardized light box set up. Higher density of sampling for *E. johnstonei* is reflective of the abundance of the species, particularly in human-altered habitats, and a desire to fully characterize the distribution of dorsal patterns present on the island. In addition, all frogs will be swabbed to test for the skin pathogen chytrid fungus *Bd* following an established protocol (Amphibiaweb: amphibiaweb.org/chytrid/swab_protocol.html). We will sample up to 10 individuals of *T. oskrobapreinorum* and 25 each of *S. sputator* and *S. parvus* throughout the islands. Lizards will be captured either by hand or through lizard-noosing. If permitted, we request the ability to humanely euthanize up to five individuals of each

species to be prepared as museum specimens to be housed at the Museum of Vertebrate Zoology (Table 1). Museum specimens will provide valuable morphological vouchers allowing for detailed analyses through x-rays and CT-scanning to determine morphological differences across islands that may be characteristic of distinct populations or species. However, we recognize that destructive sampling may be undesirable and defer to the judgement of the Nature Foundation Sint Maarten. All other individuals sampled for this study will be released alive. Each individual will be photographed and tissue. Lizards will be tissue via tail clip at natural break plains and frogs will be tissue by shallow toe-clip following aseptic technique. Tissues will be preserved in RNAlater for shipment to the United States.

For invasive species, we will conduct similar sampling protocols. We propose to sample to 25 individuals of each species. Frogs will be captured by hand, swabbed for Bd, and tissue. *Hemidactylus mabouia* will be captured by hand or lizard-noosing technique. Blood samples will be taken from lizards in addition to tail tissue to examine for evidence of squamate malaria. Because invasive species are often undesirable to the local ecosystem, we will humanely euthanize all captured invasive individuals following protocols approved by the University of California Institutional Animal Care and Use Committee. If euthanized, a subset of five animals will be prepared as museum specimens and for educational and scientific purposes at the Museum of vertebrate Zoology or donated to the Nature Foundation Sint Maarten. Alternatively, these individuals may also be re-released alive if desired by the Nature Foundation Sint Maarten.

We will sequence samples using restriction-site associated DNA sequencing (RAD-seq) (Miller et al. 2007). This high-throughput protocol will generate single nucleotide polymorphisms (SNPs) distributed throughout the genome of each species allowing for analysis of genetic diversity while controlling costs. All genetic analysis will take place at the University of California, Berkeley. We will analyze our RAD-seq generated SNP data to understand the evolutionary history of each species. In brief, we will reconstruct phylogenies for each species representing how various populations throughout the Lesser Antilles are related to each other and the mainland. We will then conduct demographic modeling to infer the population demographic history of each species. This will allow us to infer routes of colonization and genetically distinct populations, as well as source populations of potential non-native populations. Additionally, we will examine phylogeographic patterns within each island to identify distinct within island lineages and to understand how geologic history may have played a role in generating population genetic structure.

Preliminary Data: We have previously sampled all three focal taxa on the island of Montserrat, Sint Eustatius, Saint Kitts, and Nevis following similar protocols to those described here. These tissues have yielded high quality DNA and have been used to optimize laboratory procedures. Additionally, we have requested museum-held tissue vouchers from across the mainland native range of *T. rapicauda*, as well as offshore Venezuelan islands and Trinidad, in order to examine routes of colonization of the Lesser Antilles from the mainland. We have also acquired representative samples of *E.*

johnstonei from collaborators from throughout the Lesser Antilles including Sint Maarten, Guadeloupe, Dominica, Martinique, St. Lucia, St. Vincent, Grenada, and Barbados. However, our present sampling on Sint Maarten is limited both in sample size ($N = 5$) and geographic distribution. Our data suggest two potential major lineages of *E. johnstonei* (Fig. 2). Combined with our existing and upcoming sampling, tissues collected from Sint Maarten will allow for detailed comparative phylogeographic study of these taxa.

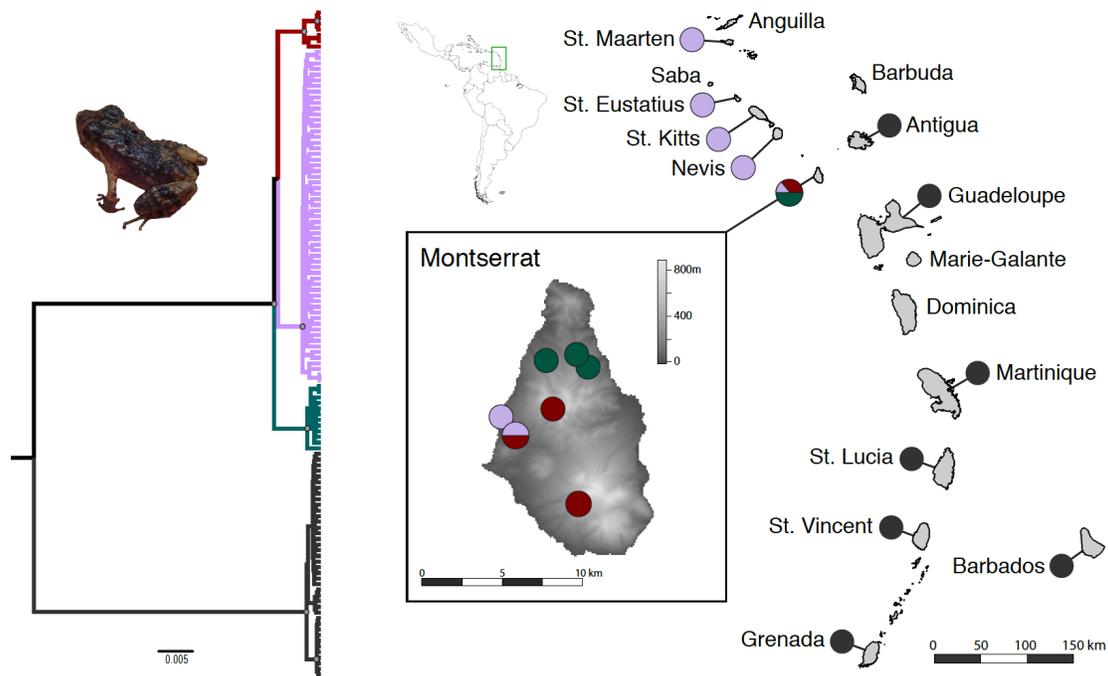


Fig. 2 Left: mitochondrial (12S and Cyt-b) phylogeny of *E. johnstonei* throughout the Lesser Antilles. Grey dots represent nodes with posterior support greater than 0.95. We recovered two major clades separated between Antigua and Montserrat. The island of Montserrat is divided into three lineages in which all other northern island populations (St. Kitts, Nevis, St. Eustatius, and St. Maarten) are nested within. Right: sampling map denoting the proportion of sampled individuals corresponding to mitochondrial lineages.

Broader Impacts: As with samples collected for Study #1, data from our phylogeographic studies will be used for both will be used for non-commercial scientific research and public outreach. Understanding the colonization of the Lesser Antilles will provide valuable scientific insight into the evolutionary history of this biodiversity hotspot. Notably, we hope to help understand the idiosyncrasies of species distributions in the region and how it relates to species traits and the geologic history of each island. Additionally, our data will be relevant to conservation concerns. With the description of a new species of *Thecadactylus* on Sint Maarten (Koehler and Vesely 2011), new concerns have been raised about potential cryptic diversity across the Lesser Antilles. We hope to help resolve the species status of *Thecadactylus* throughout the region to allow for more effective conservation planning. For *E. johnstonei*, our data will contribute to our understanding of its native range, which is currently in dispute (Kaiser 1997). As a highly

invasive species in some regions (Kaiser 1997), knowledge of which islands were colonized naturally and which islands represent modern invasions is fundamentally important to how the species is managed at a local level. Lastly, our phylogeographic data will also provide information on evolutionarily distinct populations within a species (Moritz 1994) and characterize population genetic diversity on the island, which may provide valuable information to the Nature Foundation Sint Maarten.

Although we (listed investigators) do not directly study disease ourselves, with the permission of the Department of Environment, we will collect blood samples (separated from tail clips) and frog skin swabs to maximize the potential data from each individual. With permission, these samples will be utilized by direct collaborating investigators specializing in amphibian and reptile diseases to facilitate the generation of useful knowledge from these samples. Any publication stemming from this proposed research, including disease studies published by our collaborators which utilize our samples, will be provided to the Nature Foundation Sint Maarten as free PDFs.

Table 1 Requested maximum sampling from Sint Maarten for each species. IUCN Red List status is listed if known and native to the island. Whole specimens will only be taken with explicit permission from the Nature Foundation Sint Maarten. Alternatively, sampling will be restricted to only non-lethal techniques including tissue sampling.

Species	Status	Tissue Sample	Whole Specimen*
<i>Anolis gingivinus</i>	Not Evaluated	50	10
<i>Anolis pogus</i>	Vulnerable	50	0
<i>Eleutherodactylus johnstonei</i>	Least Concern	25	5
<i>Thecadactylus oskrobapreinorum</i>	Not Evaluated	10	5
<i>Sphaerodactylus sputator</i>	Least Concern	25	5
<i>Sphaerodactylus parvus</i>	Not Evaluated	25	5
<i>Osteopilus septentrionalis</i>	Introduced	25	5
<i>Scinax ruber</i>	Introduced	25	5
<i>Hemidactylus mabouia</i>	Introduced	25	5

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