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Adult male Puerto Rican Dwarf Gecko, *Sphaerodactylus macrolepis guarionex*: Like other very small lizards, Dwarf Geckos struggle with heat and water loss, avoidance of which requires sophisticated exploitation of available structural, thermal, and temporal microhabitats.

Size Does Matter

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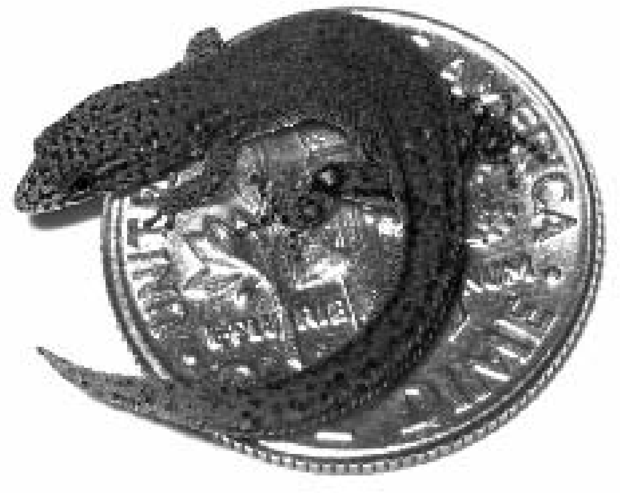
"We are prisoners of the perceptions of our size, and rarely recognize how different the world must appear to small animals."

Steven Jay Gould
Natural History, January 1974

Size of an animal is in many ways its most important biological trait. According to J.B.S. Haldane's principle, "sheer size very often defines what bodily equipment an animal must have." Lizards are a diverse group of animals with extremely diverse morphologies and biologies. Lizards vary greatly in size from the largest living lizard, the Komodo Dragon (*Varanus komodoensis*), which measures up to 3 m from head to tail, to the smallest living lizard, the Jaragua Dwarf Gecko (*Sphaerodactylus ariasae*), which measures only to 28 mm from head to tail. Many exhibit amazing adaptations relative to their sizes. However, extremes in body size can incur considerable consequences. Particularly, as size decreases, physiological functions such as water balance and heat regulation can become exigent on small lizards' biologies. Herein I discuss the physiological challenges facing Dwarf Geckos (genus *Sphaerodactylus*) and describe how these remarkable lizards not only cope, but also thrive in suitable environments.

The genus *Sphaerodactylus* is comprised of over 90 species that are widely distributed throughout the West Indies, occurring on every major island in the Caribbean, as well as in northern South America through Central America into parts of México as well as southern Florida. Species of *Sphaerodactylus* occupy a wide variety of ecosystems that range from montane rainforests and hilly scrub woods to coastal, desert-like habitats. Species range in size from 16 mm snout-vent length (SVL) to 40 mm SVL. A few species reach the lower limits of amniote body size and are considered to be the smallest terrestrial verte-



S. BLAIR HEDGES

Sphaerodactylus ariasae, discovered in 2001 on Isla Beata, a small Hispaniolan satellite island, is the smallest known amniote (a group that includes all reptiles, birds, and mammals). Extremely small body size imposes severe challenges in regard to thermo- and osmoregulation.

ALEJANDRO SÁNCHEZ

Adult male *Sphaerodactylus macrolepis macrolepis* from St. Croix, U.S. Virgin Islands: *S. macrolepis* is a polytypic species with nine currently recognized subspecies, all endemic to the Puerto Rico Bank. *Sphaerodactylus macrolepis* is the most abundant and widely distributed Dwarf Gecko in Puerto Rico. Populations in different areas exhibit great variation in morphology, microhabitat use, and osmoregulation.

brates discovered to date. Adults of the smallest species, *Sphaerodactylus ariasae*, from Isla Beata, off the southern coast of Hispaniola, can curl up on a dime! Furthermore, population densities can be phenomenally high. One species (*Sphaerodactylus macrolepis*), which is endemic to the Puerto Rico Bank, is known to reach densities to 67,000 lizards per hectare, quite possibly the highest population density for any lizard in the world!

For such tiny lizards, Dwarf Geckos exhibit considerable diversity in morphology, ecology, behavior, and general natural history — including the fact that many violate a general rule of gecko biology. Unlike most geckos, which are nocturnal, species of *Sphaerodactylus*, with only a few exceptions, are diurnal or crepuscular. Another departure from general gecko habits is that most species are ground-dwellers, with very few known to be primarily arboreal or saxicolous. The paucity of arboreal forms may be attributable to the fact that Dwarf Geckos lack the typical large flattened "toe pads" used by most other geckos for climbing. These toe pads sport tiny rows of plate-like projections called lamellae, each of which is equipped with thousands or even millions of microscopic hook-like hairs called setae. These make it possible for most geckos to climb on nearly any surface, even ceilings or vertical panes of glass. However, as the name implies, *Sphaerodactylus* (*sphaero* = round and *dactylus* = digit) feet bear round lamellae that are restricted to the tips of their toes.

These tiny lizards inhabit a variety of microhabitats in just about every type of terrestrial environment in the West Indies. They are commonly found in dense leaf litter, inside termitaria, or under dead palm fronds, agaves, fallen trees, large rock spills, and human debris, such as wooden boards and galvanized steel sheets. A few species (e.g., Jamaican *S. semasiops* and *S. oxyrhinus*) are known to occur only in the complex microhabitats of arboreal bromeliads.

The Surface Area-to-Volume Ratio

A major physiological challenge that affects all small animals is a high surface area-to-volume ratio (SA/V), which, in turn, affects basic physiological processes like osmoregulation and thermoregulation. As a lizard's body size decreases, the relative surface area increases. This increase occurs because surface area decreases as length squared, whereas volume decreases as length cubed. Consequently, volume decreases more rapidly than surface area, resulting in a high ratio. For tiny sphaerodactyls, the high SA/V has profound effects on how they live their lives and function in the environment.

Problem 1: Evaporative Water Loss

One vital challenge associated with a high SA/V is controlling water loss to the environment through evaporation. Evaporative water loss (EWL) plays an important role in the patterns of behavior and activity for lizards of all sizes, but most especially the smaller species. The rate of EWL depends primarily on three factors: Size of an animal, rate of oxygen consumed, and physical properties of the skin. Due to their incredibly high SA/V, small lizards inevitably experience very high rates of cutaneous evaporative water loss. This is particularly true of Dwarf Geckos.

SAÚL S. NAVA

Adult male *Sphaerodactylus macrolepis mimetes* from Puerto Rico: Note the toe tips with round lamellae for which the genus is named.

ALEJANDRO SÁNCHEZ

Adult *Sphaerodactylus klauberi* from a montane rainforest in southeastern Puerto Rico: *S. klauberi* is endemic to Puerto Rico and is one of the larger species of Dwarf Gecko, reaching sizes to 39 mm SVL. This species is found only in mesic, montane habitats.

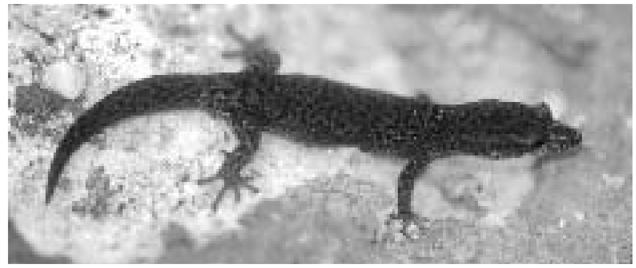
In the few EWL studies on *Sphaerodactylus*, researchers found that these lizards exhibit incredibly high rates of EWL. In fact, some of the rates reported for *Sphaerodactylus* are among the highest recorded for any lizard. These studies suggest that, in comparison to other lizards inhabiting similar or identical environments, Dwarf Geckos have modest physiological adaptations capable of compensating for high EWL. Additionally, EWL rates are generally higher for reptiles inhabiting humid habitats than species inhabiting arid habitats. In terms of humidity, species of *Sphaerodactylus* occupy all types of environments. Some, like *S. klauberi*, which is endemic to Puerto Rico, are found only in very mesic (moist) montane ecosystems, whereas others, such as *S. parkeri*, from Jamaica, occupy xeric (dry) coastal environments that have all of the characteristics of deserts. Although all species demonstrate high EWL rates, one study found that eggs of *S. cinereus*, a Hispaniolan form, might have the lowest EWL rate of any reptilian egg. More research on EWL of eggs is needed to further explore this adaptation.

Problem 2: Thermoregulation

Thermoregulation is also difficult when faced with a high SA/V. Dwarf Geckos are poikilothermic, meaning that they have no internal metabolic mechanism for regulating body temperatures, which consequently vary with the environment. As in any small-bodied animal, heat is gained and dissipated relatively rapidly, negating any ability to effectively regulate body temperatures using behavioral mechanisms, such as those used with amazing efficiency by many larger reptiles. Large surface areas result in greater exposure, and the relatively small body volume retains heat ineffectively. Thus, sphaerodactyls are extremely vulnerable to heat stress. On the other hand, unlike larger lizards, Dwarf Geckos absorb heat rapidly, and, unlike most larger forms, do not need to bask in order to raise their temperatures. The net effect, however, is that these diminutive species cannot effectively deal with variations in environmental temperatures.

The Solution: Microhabitat Selection

So, what defenses do Dwarf Geckos have against dehydration or heat stress imposed by their diminutive sizes? Although evidence shows that their bodies are not adapted physiologically to min-



ROBERT POWELL

Sphaerodactylus parvus, from Anguilla: This species can attain huge population densities in suitable habitats.

ALEJANDRO SÁNCHEZ

A Cosmopolitan House Gecko (*Hemidactylus mabouia*) from Tortola, British Virgin Islands. This gecko is widely distributed in the West Indies. Although much larger, House Geckos may share communal nests with Dwarf Geckos and often are found cohabitating under large rocks, fallen trees, and logs.

ALEJANDRO SÁNCHEZ

Adult *Sphaerodactylus nicholsi* from the Bosque Seco, an extremely arid region in southwestern Puerto Rico: This species is the smallest Dwarf Gecko endemic to Puerto Rico and lives in sympatry with the much larger *S. roosevelti.*

Adult female *Sphaerodactylus roosevelti* from the Bosque Seco in Puerto Rico: This species reaches sizes to 39 mm and is active predominantly at night. Like many, but not all Dwarf Geckos, *S. roosevelti* is sexually dimorphic. Note the prominent dorsal stripes, a characteristic seen only in females of this species.

imize water loss and maintain suitable body temperatures, sphaerodactyls can overcome these limitations by behaviorally exploiting microhabitats often unavailable to larger species. Microhabitat selection is undoubtedly the best defense against dehydration and overheating. Most of the terrestrial habitats occupied by these lizards are relatively heterogeneous regarding humidity, and individuals of most species occur under a variety of complex substrates that appear to preserve high humidity levels. Several studies on Dwarf Gecko ecology have shown that the two most important factors in microhabitat selection are relative humidity and structural complexity. For example, *S. parvus*, endemic to the Anguilla Bank, demonstrates a clear preferential use of microhabitats, such as large rocks shaded by dense forest canopies that provide effective insulation from overheating. Additionally, leaf litter on the forest floor, for example, can be relatively deep and dense, sometimes greater than a meter in depth. This type of substrate provides an ideal microclimate in which relative humidity levels are substantially higher than ambient humidity. Microhabitat selection extends also to aspects of reproduction in Dwarf Gecko ecology. Nest sites are invariably established in humid, sun-sheltered microhabitats (e.g., under large, fallen trees, logs, or large rocks). Moreover, Dwarf Gecko eggs are commonly found in communal nests (one nest site where multiple females lay eggs), often with eggs of other species and genera (e.g., *Hemidactylus* spp.). Even in arid environments, Dwarf Geckos typically are found in the most humid and appropriate microhabitats, usually under trees or cover — access to which is possible only because of their small sizes. For example, in Puerto Rico's "Bosque Seco" (dry forest), which is in essence a desert, *S. nicholsi* and *S. roosevelti*, are typically found in the leaf litter underneath Sea Grape trees, which is substantially more humid than the ambient climate. By actively selecting microhabitats that preserve humidity, these lizards can endure and even thrive in very arid environments. Additionally, many species restrict activity to twilight hours, times of day when ambient temperatures are less severe. Although not common among species of *Sphaerodactylus*, presumably because most forms can effectively exploit the "right" microhabitats, some species, like *S. roosevelti* from Puerto Rico, *S. parkeri* from Jamaica, and *S. sputator* from the Anguilla and St. Christopher banks, have opted for nocturnal lifestyles, reducing even more their exposure to daytime heat and the consequent danger of dehydration.

Conclusion

> "For every type of animal there is a most convenient size, and a large change in size inevitably carries with it a change of form."
> J.B.S. Haldane, 1928

Despite physiological challenges imposed by diminutive size, geckos in the genus *Sphaerodactylus*, like many other small animals, must rely on behavioral and ecological strategies to survive. Dwarf Geckos overcome the challenges of desiccation and heat stress by actively selecting the least dehydrating microclimates available in their macroenvironments. So, the small size that is

Adult male *Sphaerodactylus roosevelti* from the Bosque Seco in Puerto Rico: Note the reduced prominence of dorsal stripes, which is characteristic of males.

disadvantageous in the context of physiological responses to the environment is the very thing that facilitates the exploitation of microhabitats, enabling these tiny lizards to survive and successfully radiate across the West Indies. Consequently, I can add to Haldane's principle that size "defines what bodily equipment an animal must have" the caveat that size also defines what behavioral responses an animals must use.

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