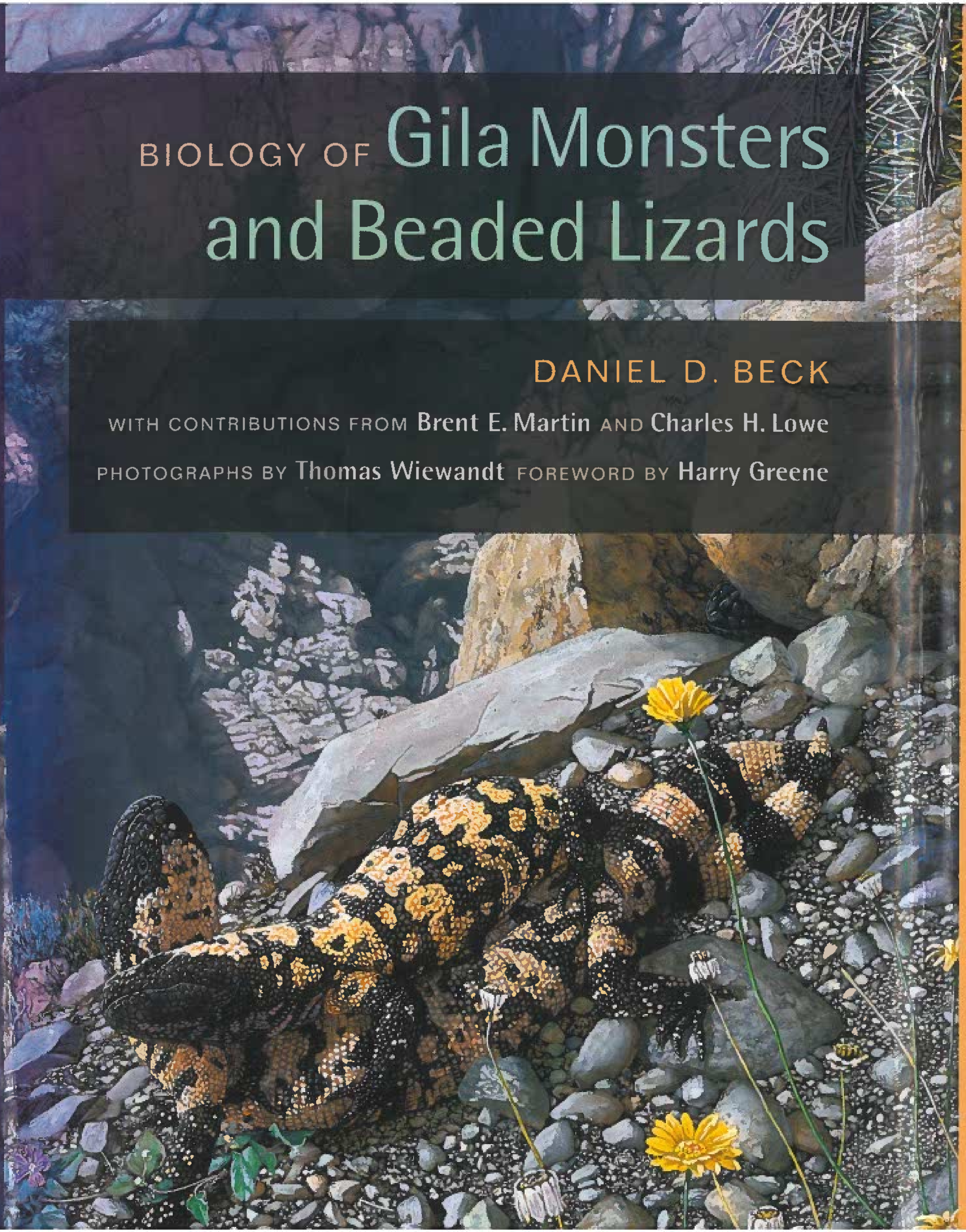
BECK Biology of Gila Monsters and Beaded Lizards CALIFORNIA



BIOLOGY OF Gila Monsters and Beaded Lizards

DANIEL D. BECK

WITH CONTRIBUTIONS FROM Brent E. Martin AND Charles H. Lowe

PHOTOGRAPHS BY Thomas Wiewandt FOREWORD BY Harry Greene

No two lizard species have spawned as much folklore, wonder, and myth as the Gila Monster, *Heloderma suspectum*, and the Beaded Lizard, *H. horridum*—the sole survivors of an ancient group of predacious lizards called the Monstersauria. More like snakes on legs, monstersaurs are a walking contradiction: they are venomous yet don't appear to use their venom for subduing prey; their mottled patterns mingle with the broken shadows and textures of their desert and tropical dry forest habitats, yet their bright open mouths hiss a bold warning that a nasty bite awaits those who advance further. And while Gila Monster venom produces excruciating pain, it also contains a peptide that has become a promising new drug for treating type-2 diabetes. Perhaps the ultimate paradox is that monstersaurs are among the most famous of lizards, yet until quite recently they have remained among the least studied. With numerous illustrations, stunning color photographs, and an up-to-date synthesis of their biology, this book explains why the Monstersauria seems poised to change the way we think about lizards. Daniel D. Beck—who has been investigating Gila Monsters and Beaded Lizards for over 22 years—teams up here with award-winning wildlife photographer Thomas Wiewandt to produce a comprehensive summary of this small but remarkable family of lizards.

Beck describes how monstersaurs are a textbook example of reptilian life in the slow lane. He explains that their capacity for large meals, ability to store energy as fat in their sausage-shaped tails, and low metabolic rates allow them to subsist for long periods without feeding. Inhabitants of the southwestern United States, western Mexico, and Guatemala, helodermatid lizards deliver a bite with a lockjaw tenacity that qualifies them as the pit bulls of the lizard world. Beck reveals that the skull morphology of *Heloderma* appears to have changed little in 23 million years, prompting paleontologists to dub it a "living fossil." Both wide-ranging and thorough, this book with its wealth of fascinating information about the ecology, physiology, and behavior of the Helodermatidae will reshape our thinking about reptilian life.

THOMAS WIEWANDT

DANIEL D. BECK is Professor of Biology at Central Washington University.

Jacket design: Sandy Drooker

Jacket illustrations: Front cover: Male Gila Monsters in combat, with female in nearby shelter; painting by Carel Pieter Brest van Kempen. Back cover: Gila Monster in southern Nevada desert; photo by Thomas Wiewandt.

"This is the first comprehensive treatment of the biology of the Monstersauria in nearly 50 years, during which time our knowledge has increased dramatically. It gives the reader an unprecedented opportunity to understand the evolution, ecology, and behavior of Gila Monsters and Beaded Lizards, as well as insights into folklore, venom, and threats to the existence of these fabled animals." —**WILLIAM COOPER**, Indiana University-Purdue University at Fort Wayne

"Beck is the foremost authority on these animals and has published extensively on them. He provides a highly readable and fascinating summary of their biology." —**JONATHAN CAMPBELL**, author of *Venomous Reptiles of Latin America*

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BIOLOGY *of* GILA MONSTERS *and* BEADED LIZARDS

With good wishes,

Daniel D. Beck

With Contributions from
Brent E. Martin and Charles H. Lowe
Foreword by Harry Greene
Photographs by Thomas Wiewandt

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Cover photograph: Male Gila Monsters in combat, with female in
nearby shelter, painted by Carel Pieter Brest van Kempen.

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A quarter of the royalties from this book will be donated by the author to the Tucson Herpetological Society to help fund education and conservation projects on reptiles and amphibians.

FOREWORD

Harry W. Greene

This book is the ninth volume in the University of California Press series on organisms and environments. Our unifying themes are the diversity of plants and animals, the ways in which they interact with each other and with their surroundings, and the broader implications of those relationships for science and society. We seek books that promote unusual, even unexpected connections among seemingly disparate topics, and we want to encourage projects that are distinguished by the unique perspectives and talents of their authors. Previous volumes in our series have spanned the ecology of Arizona grasslands, the behavior of Bornean treeshrews, and Seri ethnoherpetology.

Biology of Gila Monsters and Beaded Lizards is an insightful, highly readable account of two species that hark back to the Age of Dinosaurs. As it turns out, the surviving members of the venomous Helodermatidae (from Greek words for "nail-studded skin") are easily weird enough to warrant such detailed scrutiny, and with familiarity, they can even provoke our admiration. One of my favorite experiences as a field biologist involved a Sonoran Desert Gila Monster, all the more so because nothing I'd ever seen or read prepared me for her singularly reptilian countenance. This was no noisy bird or stinky mammal! Neither fast nor particularly slow, arguably awkward in stride, "Laura" (the subject of a friend's research, informally named after his wife) seemed to be headed for somewhere in particular. She moved among the trunks of saguaro cacti and palo verde trees with a curiously lumbering gait, advancing over the rocky terrain perhaps twenty body lengths in the course of five minutes; every few seconds her black forked tongue flickered out, and occasionally she paused to turn her head this way, then that. In gestalt she looked like a blunt-snouted, short-tailed version of the closely related, Old World monitor lizards. Even with binoculars I could scarcely make out her little helodermatid eyes, hidden among equally dark head scales, and thus viewed up closely, her body looked like a variegated patchwork of tiny black and pink, perfectly round pebbles. Academic deadlines and global politics faded from my mind as I watched Laura navigate her homeland. In this Gila Monster morning there were quail eggs to be found, coyotes and badgers to avoid; there might be potential mates to evaluate before she sought shelter from the midday sun. And later in the year, if things went well, there would be her own nest burrow to construct.

Today Gila Monsters and Beaded Lizards are the only venomous species among roughly four thousand kinds of lizards worldwide. Scientists first described helodermatids in the mid-1800s and for more than a century their only claims to fame were venom and a restricted North American distribution. As popular zoo exhibits, captives fed a steady diet of chicken eggs would survive for years in an abnormal state of lethargic obesity, but until recently their natural history remained obscure for lack of study. Now a wealth of research demonstrates that these stocky creatures, in many ways unlike even other large lizards, are hardly the sluggish brutes of earlier texts. Their toxic saliva is used primarily for defense rather than feeding and has yielded unexpected applications in human medicine. From an evolutionary viewpoint, helodermatids are justly labeled "living fossils" because they are the sole remnants of an ancient, cosmopolitan lineage that has changed relatively little over tens of millions of years. Often misleadingly described as strictly nocturnal and highly sedentary, they are champion diurnal walkers, sometimes covering a mile in as little as four hours when the urge to travel hits. They are specialized vertebrate nest predators, and like skunks, armadillos, and other so-called preoccupied foragers, helodermatids are unusually well protected. And they seem to have an adaptable, working familiarity with their surroundings—Gila Monsters and Beaded Lizards typically behave as if they have some sort of plan.

We know these things about helodermatids and much more primarily thanks to studies by the late Charles H. Lowe and his associates at the University of Arizona, and among the latter, especially Daniel Beck. A clever, tenacious, and widely experienced field biologist, for more than 20 years Dan has studied Gila Monsters in Utah, Arizona, and New Mexico as well as Beaded Lizards in Mexico. In this book he lucidly synthesizes all available information on these creatures and their kin, from paleontological history and the etymology of vernacular names to venom biochemistry and population ecology. Dan is a fine, scholarly writer with an unusual ear for storytelling, as exemplified here by his explanation of how a meal of young rabbits, comparable in relative weight to the world hot dog-eating record in humans, might last a Gila Monster for more than a third of a year. *Biology of Gila Monsters and Beaded Lizards* is also wonderfully illustrated by numerous black-and-white and color images, many of them by award-winning Tucson photographer Thomas Wiewandt. Tom has a painter's eye for color and form, as well as a Ph.D. zoologist's appreciation for organisms in their environments, and his pictures provide a subliminal feel for these crusty, oddly beautiful animals as they are in nature.

Research inevitably leads to more questions, even as what we have already learned yields diverse applications, and Dan Beck notes in his closing chapter that much remains to be studied about almost every aspect of helodermatid biology. The behavior of young animals remains a mystery, for example, and I suspect that someone with the patience to observe individual adults for long periods will make surprising discoveries about their cognitive abilities. In the meantime, helodermatids are still fairly common in some areas and reasonably likely to be encountered at the right time, in the right season. Far from being slothful and boring, they are among the world's great herpetological wildlife sights. My fondest hope is that beyond the obvious scientific and conservation value of *Biology of Gila Monsters and Beaded Lizards*, Dan Beck's prose and Tom Wiewandt's images will inspire readers to go see them in the wild, to care about their persistence.

November 2004

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If it takes a village to raise a child, bringing up this book required a real community. Foremost in that community is my best friend, personal editor, academic advisor, and hero, Kris Ernest, who took up the slack for me from many hours of neglected duties at home, suffered through each draft of the book, picked me up when I stumbled and grumbled, and still remained married to me. Her steadfastness rivals that of *Heloderma*.

Others among my home-based support center are my good friends John, Anne, and Gabe Merrill-Steskal (who encouraged me, fed me, and even gave me an office in which to finish this book at the same time we were building our house); Mark Larson; Carey Gazis; and Jeff Hashimoto. My kids, Abby and Langdon, provided entertainment and perspective, while helping me stay centered and focused on priorities. The rest of my family, Leia Beck, Jon Beck, John and Sue Ernest, and Holly Ernest, offered additional, crucial doses of understanding, encouragement, and support.

Members of the Department of Biological Sciences at Central Washington University deserve credit for taking up the slack during the sabbatical in which I began writing this book and for putting up with me as I finished the writing after my return. Members of the Tucson Herpetological Society provided encouragement and support both during my sabbatical in Arizona and in later stages of book preparation.

Special thanks are due to Doris Kretschmer of the University of California Press, who patiently guided this naïve author through all the tortuous trials of writing a book—from initially encouraging me to submit the book, to negotiating a contract, and through all the later stages of production. Scott Norton, of the University of California Press, skillfully coordinated the art program of the book. I also appreciate the efforts of the staff at TechBooks in York, Pennsylvania: Joanne Bowser, who oversaw the production of the interior of the book from manuscript to final printer files; Cheryl Uppling, who copyedited the book; and Tony Moore, who coordinated the editorial process.

A vast community of colleagues stepped up to help bring this book to fruition. Jon Campbell, Eric Coombs, William Cooper, Dale DeNardo, Harry Greene, and Brent Martin read the entire book and provided valuable feedback. Many colleagues provided helpful comments on chapter drafts; they include: Randy Babb, Mike Douglas, John Eng, Kris Ernest, David Hardy, Randy Jennings, Steve Mackessy, Bob McCord, Eric Pianka, Roger Repp, Phil Rosen, Gordon Schuett, Brian Sullivan, Tom Van Devender, Tom Wiewandt, and Andrew Young.

Many colleagues provided unpublished data and observations. They include Stephen Angeli, Robert Applegate, Randy Babb, Andrew Barnum, Kent Beaman, Don Boyer, Dale DeNardo, Jerry Feldner, Leticia Gallardo, Andrés Garcia-Aguayo, C.M. Gienger, J. Hanson, Jim Jarchow, Jeff Lovich, Charles H. Lowe, Brent Martin, Brian McGurty, Ann McLuckie, Antonio Ramírez, Aurelio Ramírez-Bautista, Roger Repp, Chris Rieman, Todd Rowe, Gordon Schuett, Mark Seward, and Brian Sullivan. Jude McNally of the Arizona Poison Control System provided information on Gila Monster bite case histories. George Goode and the Tucson Rural Metro Fire Department provided records of human–Gila Monster encounters in Tucson, Arizona. Randy Babb of the Arizona Department of Game and Fish provided Gila Monster encounter records.

Through conversations, correspondence, and interviews, many have helped clarify my understanding of helodermatid lizards. If I omit anyone from the following list who belongs in this category, it is not intentional: Stephen Angeli, Robert Applegate, Randy Babb, Andrew Barnum, Kent Beaman, Charles M. Bogert, Joe Branham, David E. Brown, Jonathan Campbell, Mike Coffeen, Eric Coombs, Kerry Crowther, Dale DeNardo, Mike Douglas, John Eng, Lee Fitzgerald, Oscar Flores, Ted Garland, C.M. Gienger, Jim Glenn, Steven R. Goldberg, Harry Greene, David Hardy, Randy Jennings, Hans Koenig, Charles H. Lowe, James A. MacMahon, Brent Martin, Brian McGurty, Charlie Painter, Eric Pianka, Lauren Porzer-Kempner, Antonio Ramírez, Aurelio Ramírez-Bautista, Roger Repp, Phil Rosen, Todd Rowe, Gordon Schuett, Cecil Schwalbe, Mark Seward, Brian Sullivan, Tom Van Devender, Tom Wiewandt, and Andrew Young.

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A community of talented and skillful artists produced the images you see in this book. Carel Pieter Brest van Kempen's amazing painting of two male Gila Monsters wrestling in combat (while a female waits in a nearby shelter) graces the dust jacket. Dennis Caldwell's skillful photographic editing brought to life the color "portraits of populations" depicting the dorsal patterns of 83 individual Gila Monsters and Beaded Lizards. Dennis painstakingly removed the backgrounds and scaled each image shown in those plates. Dennis also helped prepare plates 19 and 27 and figure 56, and he created the fine pen and ink drawings shown on page iii. The artwork of Randy Babb also graces several pages of this book including the color drawing of mating Gila Monsters (plate 32). Randy put great effort into drawing from dissections images of the venom apparatus (figs. 9, 10, and 11) shown in chapter 3. Russell Duncan helped produce the map of Gila Monster–human encounters near Tucson, Arizona (fig. 56), and Andrés García-Aguayo provided the maps of Mexico shown in figure 55. The financial generosity of Amylin Pharmaceuticals helped to defray the costs of bringing many of these beautiful images into the book.

Others provided photographs for the "portraits of populations" images. They include: Carlos Balderos, Dennis Caldwell, and Tom Wiewandt (plate 13); David Adcock, Don Boyer, and Gordon Schuett (plate 14); C.M. Gienger and Ann McLuckie (plate 15); Brian Sullivan and Brent Martin (plate 16); and Mike Hill and Bill Radke (plate 18). Matt Goode donated the spectacular photograph of a king snake eating a juvenile Gila Monster (plate 30).

The person most responsible for the stunning photographs in this book is Tom Wiewandt of Wild Horizons. Although Tom's photographs speak for themselves, I must say, I am very honored to have his work compose such a significant portion of this book. Tom and I worked very hard to capture images of helodermatid lizards doing exciting things in nature (rather than inanimate-looking portraits of torpid lizards lying motionless, which are the usual images helodermatids tend to provide). Many people helped us capture those images (also see Tom's separate acknowledgments). I'll mention here the hospitality of Carlos Guichard Romero and Antonio Ramírez at ZooMAT in Tuxtla Gutiérrez, Chiapas, who hosted us in October 2001. Antonio patiently worked with us for a solid week to make the photographs you see in plates 2, 4, and 19. Others who deserve special credit for helping to make Tom's photographs are Joe Branham, C.M. Gienger, Ann McLuckie, and Mark Seward.

For inspiration at various stages of this work, I thank Jon Campbell, Ken Dodd, Harry Greene, Vic Hutchison, Charles Lowe, James MacMahon, Eric Pianka, Richard Shine, and Laurie Vitt. For the parts that read well, credit is due to my skillful editors (Joanne Bowser, Kris Ernest, Doris Kretchmer, Tony Moore, Cheryl Uppling, and the colleagues mentioned above who read drafts of the book). For parts that might remain awkward, well, a good editor can only do so much. And despite all the hard work and attention to detail, this book admittedly leaves many gaps to fill, revealing barely the surface of a mountain of knowledge that awaits discovery. Despite the best efforts of my colleagues, errors and omissions remain inevitable, and I stand solely responsible for those shortcomings.

This work is dedicated to those who guided me on the path to this book, my mentors; Jim MacMahon, Jim Glenn, Chuck Lowe, and my father, Ted Beck. I also dedicate this book to my students, future researchers, and colleagues who will take us to new levels of insight about our only venomous lizards. Finally, I dedicate the book to the children, our future generations: may they grow up to enjoy the wonders of all things helodermatid, and inherit a world that retains a lot of creepy crawly creatures from which to learn.

Daniel Beck, Ellensburg, Washington,
November, 2004

PHOTOGRAPHER'S ACKNOWLEDGMENTS

Capturing the character of an animal on film is what wildlife photography is all about; and after working with Gila Monsters and beaded lizards for more than three years, I rate these reptiles as among the most challenging subjects I've tackled during the past thirty-five years. They are masters at striking a "lifeless" pose. Their dark, beady faces obscure their beady, black eyes—the proverbial "windows to the soul." And because of their secretive and sedentary ways, much of the photography for this book had to be done under carefully controlled conditions. Keeping such images authentic to nature would have been impossible without the expertise and assistance generously offered by friends and colleagues along the way.

First and foremost, I thank Dan Beck, who graciously invited me to participate in this monumental project and spent several weeks photographing with me in Mexico and the United States. He and his former student Chris Gienger welcomed me in their study areas, gave me a hand with the photography, and opened doors to other important photographic opportunities.

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Thomas Wiewandt, Tucson, Arizona
www. wildhorizons.com

CHAPTER 1

Monsters in Our Midst

HISTORY, HUMANS, AND *HELODERMA*

> He's a walkin' contradiction. Partly truth and partly fiction . . .
>
> KRIS KRISTOFFERSON

INTRODUCTION

There are hundreds of species of venomous snakes, yet only two lizard species are known to be venomous. These lizards belong to the family Helodermatidae, which consists of but one genus, *Heloderma*, a term derived from the Greek words *helos* for "nail stud" and *derma* for "skin." This is an apt description of the studded skins of helodermatid lizards, which are embedded with bony, beadlike osteoderms (plate 1). The specific epithets *horridum* (the horrible one), for the Mexican Beaded Lizard (plate 2), and *suspectum* (the suspect), for the Gila Monster (plate 3), suggest a more sinister side. As they do with venomous snakes, humans have historically regarded helodermatid lizards as loathsome and dangerous, reminding us of the dark side that lurks in the shadows, both in nature and in our imaginations. But, because they are *lizards*, the archetypal fear of snakes that lies embedded in the human psyche does not fully extend to *Heloderma*. They don't slither; they walk. Even though bumpy lizards are venomous, most people do not perceive the same sinister threat from them as they do from snakes.

Nonetheless, the development of our knowledge about helodermatid lizards mirrors our discovery and gradual understanding of all things sinister and misunderstood. First there are fantastic tales of pain, horror, and death, accompanied by fear and repugnance. Size and dangerousness are often exaggerated. There is fierce debate. Facts may be ignored. As we learn more, fear is replaced with respect—a respect that, in the case of *Heloderma*, has blossomed into full-blown fascination. No other species of lizards have spawned as much folklore, wonder, and myth as those of the Helodermatidae. And new discoveries about this small but remarkable family of lizards are even more intriguing than the folklore.

Helodermatid lizards share a more recent common ancestor with snakes than they do with most other lizards. More like snakes on legs, helodermatid lizards are indeed a walking contradiction. These lizards probably shouldn't still be here. Most other genera on the earth 23 million years ago have either moved on to extinction or evolved into new lineages. Helodermatid lizards present a number of paradoxes. They are venomous, yet they don't appear to use their venom for subduing prey, as do nearly all other venomous reptiles. They are at once cryptic and aposematic. Their mottled patterns of yellow/orange and black mingle with the broken shadows and textures of their desert and tropical dry forest habitats (plate 4). But approach more closely and the cryptic pattern is transformed into a bright, bold BEWARE: a wide-open mouth—soaked in venom—hisses a warning that a very nasty bite awaits those who advance further (plate 5). The bite is delivered with a lockjaw tenacity that surely qualifies *Heloderma* as the pit bull of the lizard world (plate 6).

Tenacity is also reflected in their evolutionary history—they are survivors. Helodermatid lizards have been placed by taxonomists in an ancient group, the Monstersauria, that dates back nearly 100 million years to the Middle Cretaceous. Helodermatid lizards roamed alongside tyrannosaurids in what is now Utah. In Mongolia, fossils of helodermatid lizards have been unearthed with nests of protoceratopid dinosaurs, upon whose young they may have fed (plate 7). The skull morphology of *Heloderma* appears to have changed little in 23 million years, prompting paleontologists to dub it a "living fossil."

Gila Monsters and Mexican Beaded Lizards present a textbook example of reptilian life in the slow lane. Their keen chemosensory abilities and excellent memories allow them to forage on vertebrate eggs and nestlings, a feeding niche shared by very few other lizards (plate 8). They must search far and wide to find such prey yet they spend the vast majority of their time resting in shelters. Their ability to eat large meals and to store energy as fat in their sausage-shaped tails as well as their low metabolic rates (*Heloderma* has among the lowest resting metabolic rates of any lizard measured) allow them to subsist for long periods without feeding.

The low-energy lifestyle of helodermatid lizards stands in stark contrast to their remarkable capability for aerobic activity and endurance. They cannot quickly sprint to escape danger, as can most other lizards, but they can walk for hours at speeds much greater than their normal foraging pace in nature. *Heloderma* has among the highest aerobic capacities of any lizard measured (chap. 4). Endurance and high aerobic capacities seem puzzling traits for slow-moving lizards like *Heloderma*, until one considers behaviors other than foraging. Male helodermatid lizards vie for access to females by performing spectacular combat rituals, reminiscent of the entwining combat dances of viperid snakes (plate 9). These tests of dominance may continue for hours, pushing the combatants' physical abilities to the limit. Males with greater endurance may more frequently emerge victorious from combat rituals and thereby enjoy greater reproductive success.

The ecology, physiology, and behavior of the Helodermatidae have helped us refine our thinking about reptilian life in the slow lane. Their odd fighting rituals, energy efficiency, and venom system are changing our views on what it means to be a lizard (Beck 2004).

Perhaps the ultimate paradox is that the Helodermatidae are among the most famous of lizards, yet until quite recently they have remained among the least studied—and least understood—lizard families in nature. Even today, we still don't know the full story of their nesting biology. Gila Monsters lay their eggs in summer, but hatchlings do not emerge until the following spring, no earlier than late April. Debate continues over the timing of hatching: Do the eggs overwinter then hatch in spring? Or do they hatch in fall, but the hatchlings remain at the nest until emerging in spring (plate 10; chap. 8)? Throughout their range, prime habitats for helodermatid lizards are disappearing, or becoming degraded, even before we can understand specific habitat traits that are critical to their existence (plates 11 and 12; chap. 9). People have long been interested in stories of the bumpy lizard. But only recently have scientists discovered enough about the ecology, evolution, physiology, and behavior of helodermatids to show that their real biology may be even more interesting than those stories. In this chapter, I'll chronicle how we have arrived at our current understanding of these misunderstood lizards. I'll outline some of the history, discoveries, mythology, and folklore of these ancient beasts. In addition, I'll describe some of the ways in which scientists have investigated the Helodermatidae. This chapter is my attempt to honor those who have laid the foundation of our understanding of helodermatid lizards and to salute those who are now poised to take us to new levels.

WHAT'S IN A NAME

The first-known written record describing *Heloderma* was penned in Latin by naturalist Francisco Hernández in 1577 and translated as "the bite of this animal, though harmful is not mortal, for which reason it is more dreaded for its appearance than for its bite, and it never tends to harm anyone unless offended or provoked" (Bogert and Martín del Campo 1956). It is ironic that this original description is closer to the truth than many popular accounts that have been published in the intervening 400-plus years. Hernández mentioned that the lizard was found in the fields near Cuernavaca, Morelos, Mexico. Today this city of over a million people resides in a region whose forests have largely been converted to agriculture and urban development, although some areas of tropical dry forest habitat still remain in the southern part of the state of Morelos.

Hernández used the term *temacuilcahuya* when he described *Heloderma horridum* stating that it was a kind of "acaltetepón." *Acaltetepón* was a term applied to lizards regarded as poisonous or that looked like they might be poisonous because of their relatively large size (Smith 1969). Hernández thought there were three other poisonous lizards in New Spain, all of which he called *Acaltetepón*. Acaltetepón, or "Aztec lizard," seems to be among the more commonly repeated indigenous terms for *Heloderma horridum*, especially in western Mexico. However, *H. horridum* may be referred to as talachini or tole-chini to the Zapotec Indians of Oaxaca, as glawemma to the Chontal Indians of Oaxaca, as ciyx or siy to the Cora Indians of Nayarít, and as caltetepón, temacuil, and temacuilcahuya to other indigenous people of western Mexico (Campbell and Lamar 2004).

Throughout Mexico and Guatemala the terms *escorpión* and *lagarto enchaquirado* are the most commonly used vernaculars for *H. horridum*, which may also be called "heloderma negro." In Spanish *chaquira* means "bead," so lagarto enchaquirado translates directly to "Beaded Lizard." Raymond Ditmars apparently coined the name Mexican Beaded Lizard, which has long been the most common vernacular in English (Ditmars 1907). However, because a new subspecies of Beaded Lizard (*H. h. charlesbogerti*) was described from eastern Guatemala (Campbell and Vannini 1988), it is no longer appropriate to refer to *H. horridum* strictly as the Mexican Beaded Lizard. We now have a Guatemalan Beaded Lizard as well. Within its range in Guatemala, *H. horridum charlesbogerti* may be referred to as niño dormido—"sleeping baby" (Ariano Sánchez 2003). To the north, in Sonora, Mexico, where the ranges of both species of *Heloderma* overlap, *H. horridum* may be called escorpión negro and *H. suspectum* escorpión pintado.

The name escorpión was already in use during the early colonial period when Hernández wrote his famous essay and was likely given to *H. horridum* by early Spanish settlers. Some believe escorpión is a variation of scorpion (the stinging arthropod), which is occasionally used to describe (in both Spanish and English) anything perceived to be venomous, including lizards (Bogert and Martín del Campo 1956; Campbell and Lamar 2004). Interestingly, a defensive behavior of *Heloderma*—to back up and face a threat head-on—vaguely resembles similar behaviors shown by scorpions. In most areas where *H. horridum* are found, escorpión refers to the lizard and the term *alecrán* refers to the arthropod. In areas where *H. horridum* does not occur, escorpión may also by used to describe the arthropod. An alternative explanation is that escorpión is a modification of *escupión*, or "the spitter" (derived from the Spanish *escupar*, "to spit"). The way helodermatid lizards face a threat by vigorously hissing and throwing their heads from side to side may have led to the erroneous belief that they spit venom at an adversary.

It wasn't until 1859, nearly 300 years after Hernández's description of the Mexican Beaded Lizard, that a second species of *Heloderma (H. suspectum)* was formally described from a specimen captured near the Arizona–Mexico border. The name *Gila Monster*, however, did not come into use until the 1870s. Before that time, settlers referred to *H. suspectum* as escorpión, escupión, or simply "the spitter." Most believe the name *Gila Monster* is derived from the Gila River, which passes through southwestern New Mexico and Arizona and where many populations of *H. suspectum* reside (plate 3). Others have suggested that *Gila* is a modification of the genus name *Heloderma*, or possibly some derivation of *Helios*, for "sun." The part of the name for *H. suspectum*, *Monster*, has obvious connotations, owing to its awkward, bulky appearance and the sinister reputation of the helodermatid lizards as they were becoming known to growing human populations in the United States and Mexico. In Mexico, *H. suspectum* is known as "monstruo de Gila" or "escorpión pintado." To the Comcáac people (Seris) of Sonora, Mexico, it is called *paaza* (Nabhan 2003). The earliest use of the name Gila Monster was traced by Bogert and Martín del Campo (1956) to an article published in February 1873 by *The World* in San Diego, California. Entitled "The Gila Monster," this article built on *H. suspectum*'s reputation as a "spitter" and set that standard for many outlandish yarns that would follow. The following transcript has been often quoted:

> I've seen a lizzard what could out-pizen any frog or toad in the world . . . went after it with a stick, but the thundering thing instead of runnin' away like any nateral lizzard, squatted on its tail and spit at me. It were about three feet long, and it had yaller scales all over it, like an alligator's hide, and it were the hardest critter to kill I ever heard tell on. I knocked it over and beat it with a club until my arm ached, but I might as well have tried to cut down a mesquit tree with a blade of grass . . . the blasted lizzard never stopped spittin. I jerked out my revolver and fired four shots at it, but the balls all skipped off its tarnal hid back into the river, and at last I got it so mad I shook the pistol in the critter's face, and I'm a liar if it didn't jump at it and ketch the muzzle in its mouth, and what's more I couldn't get it away again. I pulled, and jerked, and sweat and swore, but no use; and I believe Mister Lizzard would hev pulled me plum into the river if I hadn't thought to cock the revolver and shoot it down his throat. The shot blew the body clean in two, and then I hope to die if the head and fore legs didn't get the pistol away from me, into the river and swim away with it.

This tale embodied the rich history of imaginative stories spawned in the frontier of the southwest in the late nineteenth and early twentieth centuries. During the same period, scientists were also engaged in a debate about whether the Gila Monster was really venomous. The species name *suspectum* was given to the Gila Monster by E.D. Cope in 1869 because he *suspected* it was venomous, but it was nearly 50 years later before scientists agreed that, indeed, this was true.

HELODERMA BITES AND THE WESTERN FRONTIER

Shortly after the Gila Monster received its threatening name—as scientists were still debating whether it was venomous—people were dying from its bite. Or at least that is what the stories told. Newspaper articles from the 1880s to the 1930s recounted numerous stories of pain, suffering, and death from Gila Monster bites in Arizona (see Bogert and Martín del Campo 1956 and Brown and Carmony 1991 for entertaining overviews). An alcoholic army colonel, a game warden, a showman with heart disease (who, after being bitten by a Gila Monster was given strong doses of adrenalin and digitalis to stimulate his heart, a treatment that likely killed him), an inebriated pool hall operator, an unsupervised toddler who cuddled up to a Gila Monster in a farm field—all these deaths were associated with sketchy details, poor health of the victim, bad medical treatment, or a combination thereof. What some stories lacked in accuracy, they compensated for with embellishment made more colorful with each retelling. A cowboy kills a Gila Monster and ties it to his saddle. The lizard revives to bite his assailant and, depending on the version of the story, either kills the cowboy, causes his arm to wither, or severely damages the "glands of his throat." Woodson (1947) mentioned six different reports he received about the same bite, the effects ranging from severe facial disfigurement from a bite on the nose, to no symptoms at all. There are several versions of a story about a hitchhiker who captures a Gila Monster and places it inside his shirt. At some point the Gila Monster bites the hitchhiker on his abdomen and the surprised traveler becomes violently ill. Luckily, he is picked up just in time to be rushed to a hospital where he receives medical attention and, in most versions of the story, recovers. [A more recent—and apparently true—version of this story occurred in 1986; this was the most serious bite case I could find reported in the published medical literature (Heitschel 1986), see chap. 3].

The last recorded death from a Gila Monster bite occurred in 1930. In this well-known case, a pool hall operator from Casa Grande, Arizona, was bitten on the thumb while teasing a Gila Monster. He allegedly died within 2 hours. After the case was publicized in the *Arizona Republic* newspaper, witnesses confirmed some suspicious extenuating circumstances, including the pool hall proprietor's being "quite drunk at the time" (Bogert and Martín del Campo 1956). Legitimate bites (where victims are accidentally bitten by wild Gila Monsters without poking them, picking them up, or otherwise harassing them) are rarely documented. And even some legitimate bites border on mythic. In two incredible cases, a parachutist and a motorcyclist (also referred to as a sports car driver) are reported to have been bitten after they crashed in the Arizona desert and accidentally landed in the jaws of angry Gila Monsters (Russell and Bogert 1981; Brown and Carmony 1991).

Interestingly, the mortality rate from bites by helodermatid lizards seemed to gradually decrease through the twentieth century. In 1943, Weldon Woodson, a respected authority on venomous bites, reported 15 deaths from 47 Gila Monster bite case histories between 1882 and 1939, or a mortality rate of 32% (Woodson 1943a, 1943b). Woodson mentioned the difficulties in accurately verifying these cases, noting that only one death was thoroughly investigated and that the patient also had a weak heart and "drank to excess." By 1947, Woodson reported only 29 deaths in 136 cases, or a mortality rate of 21% (Woodson, 1947), and by 1950 the mortality rate from Gila Monster bites had dropped to 14.6% (23 deaths from 158 case histories; Woodson 1950). In 1956, Bogert and Martín del Campo reported a mortality rate of 25% based on 34 case histories, but these authors noted the dubious nature of some of the reports. A summary of bite cases in 1981 mentioned no deaths whatsoever (Russell and Bogert 1981). Although medical advances in antivenins and treatment of trauma have greatly benefited snakebite patients, improved medical treatment probably does not account for the drastic drop in deaths from *Heloderma* bites since the 1930s. More likely it is that, as medical records improved, it became harder for writers to publish their embellished tales of suffering and death (Brown and Carmony 1991). By the 1990s, it was generally accepted that no person in good physical health who had been given appropriate medical treatment had ever died from a Gila Monster bite (Brown and Carmony 1991), although, in the throes of pain from a bite, some might wish they had. Chapter 3 provides an overview of recently published *Heloderma* bite case histories.

HELODERMA IN INDIGENOUS FOLKLORE

Helodermatid lizards were a source of folklore and fascination long before the colorful stories of western lore, even before Hernández described the Acaltetepón. In fact, lizards in general have long been powerful symbols in both the Old and the New Worlds. The motionless basking behavior of lizards has made them Christian symbols of contemplation; Catholic St. Gregory the Great observed that lizards symbolize the soul that humbly seeks enlightenment (Chevalier and

Gheerbrant 1994). Many native peoples, including cultures of western Mexico, believed that helodermatid lizards possessed spiritual powers capable of causing sickness. Even today, *H. horridum* appears with demonic features in carved wooden figures, or alebrijes, of Oaxaca. The Tohono O'odham, or "Desert People," who have lived in the Sonoran Desert for thousands of years, believed that an encounter with a Gila Monster, who they called *cheadagi*, could cause a person to break out in sores on the feet or body; nursing mothers could lose their milk. The remedy for such an encounter was to tie a red cloth around either the offending lizard or a suitable fetish carved from a saguaro rib. A Gila Monster song could also be sung by a shaman to correct the problem (Brown and Carmony 1991). The Pimas, closely related to the Tohono O'odham, thought that if a prospective father killed a Gila Monster, the baby's body could become red and feverish. They too sang a song as a remedy. The Comcáac people, or Seris, who live along the coast of Sonora, Mexico, understand the bite of the Gila Monster, who they called *paaza*, to be toxic. However, they also believe paaza has the ability to spit a substance (not necessarily considered toxic but capable of causing rashes) from its mouth 4 m or more (Nabhan 2003). Some make jewelry from the skin of Gila Monsters for good luck.

Some indigenous people thought that, by communicating directly with the storm spirit, Gila Monsters could control the weather. The Apaches regarded the presence of a Gila Monster as a sign of impending rain (Brown and Carmony 1991). In Mexico, I once heard an interesting story from a villager in coastal Jalisco about how Acaltetepón saved an Aztec corn crop and gained his bumpy hide. Long ago, many Aztec villages in tropical deciduous forests planted their cornfields during the hot, dry period that preceded the summer rainy season. (Many residents of tropical dry forest still do this today.) The people would then wait for quenching rains to soak their fields and nourish their corn, which, in turn, nourished and fed the people year after year. One year, after the corn had been planted, the rain did not come. The people became worried and, knowing of his reputation for bringing rain, called on Acaltetepón for help. The people persuaded the lizard to visit their cornfield (possibly by placing eggs in the field), and, after feeding on the eggs, Acaltetepón retreated to his burrow beneath the corn crop. Immediately, life-giving rains came, the corn grew fast, and the most bountiful crop the people had seen in many years was harvested from the field. And, even today, if you examine the skin of Acaltetepón, you will see small kernels of corn that cover his body, left as a reminder of his supernatural powers to affect the weather. I do not know the original source of this story, but, as with many myths, it may have some roots in reality. In Jalisco, Beaded Lizards may show an increase in activity during the dry season a few weeks before the rains arrive, and they are also frequently encountered on the surface after the first summer rains begin (chap. 5).

The Tohono O'odham explained the origin of Gila Monster's brightly colored osteoderms as an outcome of the first saguaro wine festival held long ago. Humans and animals alike were invited, and everyone wanted to look his or her best. Gila Monster came festooned with bright pebbles, gathered to make a colorful and durable coat, which is still worn to this day (Wright 1929). Perhaps it is no coincidence that the Tohono O'odham wine festival takes place in late June and early July just before the onset of the Sonoran Desert summer monsoons. With the rains, Gila Monsters (and many other desert-dwellers) may reemerge after waiting out the early summer drought.

The bony osteoderms of the Gila Monster have earned it the title of "well armored warrior of the Navajo." Old Navajo warrior tales tell of mortals who wore flint armor and looked like the Gila Monster, the protector (Hausman 1993).

HELODERMA AND HOLLYWOOD

No creature as famous and allegedly sinister as *Heloderma* could escape the imagination of Hollywood. So, in 1959, Ray Kellogg produced a low-budget horror film "The Giant Gila Monster," set in rural west Texas (fig. 1). A serious thyroid condition produces a menacing beast that attacks and kills primarily teenagers, not by crushing them in its jaws, but by stepping on them with its giant feet. A heroic teenager finally destroys the horrible lizard by loading his hot rod with nitroglycerin and sending it into the creature's open mouth. Despite the title, the footage in the movie actually shows a Mexican Beaded Lizard *(H. horridum)*, not a Gila Monster *(H. suspectum)*.

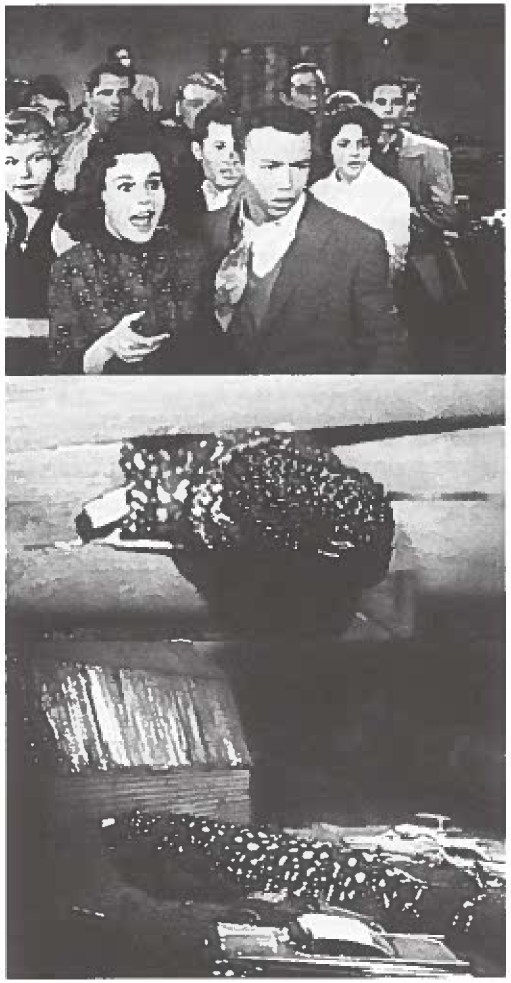


FIGURE 1. Teenagers react in horror in the film *The Giant Gila Monster* as the monster (actually a Beaded Lizard) interrupts their party. Photo credits: © 1959 Hollywood Pictures Corp. and Englewood Entertainment.

HELODERMA IN MEDICINE

Many native cultures have viewed helodermatid lizards as a source of medicine. The Yaqui people of Sonora, Mexico, believed that the skin of the Gila Monster had curative powers and, if placed over a wound or infection, would remove poison and enhance healing (Brown and Carmony 1991). The Comcáac of coastal Sonora used Gila Monster tails to treat psychosomatic illnesses and the skin, placed on a person's forehead, to treat headaches (Nabhan 2003).

The Navajos believed that Gila Monster was the first medicine man (Hausman 1993). As he crawled through the desert they say his forefoot trembled. As the original "hand trembler," Gila Monster could foretell the nature of illness and protect against it. In the Navajo story "the Flintway" (Hausman 1993), Elder Brother entered a forbidden realm of Navajo spirits and was torn apart by lightning bolts thrown by White Thunder. Old Man Gila Monster, the healer who lived at the bottom of "Earth Whirling," sang five healing songs: the song of the Black Ant, Thunder, Sun's Healing Song, the Sun and the Wind, and the Spider Web. Collectively, Old Man Gila Monster's songs wove together the broken strands of Elder Brother's shattered self and restored him to life.

Early settlers to Mexico told stories in which the Mexican Beaded Lizard held powers as an aphrodisiac. In his account of *H. horridum*, Hernández reported that "The meat of the loins of this animal, eaten in the weight of two ovulos which equals one escrupulo (1.198 mg), is said to awaken the sexual appetite better than any other known medicament" (Bogert and Martín del Campo 1956).

The notion that *Heloderma* might be a source of medicine was also entertained by Anglo settlers of the southwestern United States. In the late 1880s, *Heloderma* venom captured the interest of homeopathic practitioners. One practitioner, R. Boocock, developed a "proving" from the venom of *H. suspectum*. Provings are small doses of a substance that are experimentally administered to healthy volunteers to determine what effects, or symptoms, they produce. Based on the principle "like cures like," different doses of the substance can then be given in the hope of treating the same ailments that show up when small doses are used in the provings. Using only himself as a subject, Boocock published a painfully detailed (if not well-replicated) set of trials describing how small dosages of *Heloderma* venom taken with "sugar of milk" produced a number of symptoms. These symptoms ranged from lethargy, headaches, dizziness, and runny nose, to erection and enhanced sexual performance (Boocock 1893, 1894). The most striking symptom noted by Boocock was "an internal coldness from my heart, as if I was being frozen to death internally, and I had no way of warming myself." Boocock used the remedy on some of his patients claiming to have successfully treated a "patient with a staggering gait" and another with skin infections and swollen legs who was near death.

Through the 1890s, others showed interest in the homeopathic use of *Heloderma* venom (Lilenthal 1894; Cameron 1898), reporting that *Heloderma* might be a "valuable remedy for certain forms of paralysis" (Bradford 1895) and useful for treating "locomotor ataxia" (Case 1897, cited in Bogert and Martín del Campo 1956). Interest in the curative powers of *Heloderma* peaked as hundreds of Gila Monsters were shipped to Europe prior to World War I. In a popular article, Douglas (1910) stated that "over a hundred and fifty Monsters in lots of a dozen" had been shipped to German physicians who were using them to treat degenerative diseases of the nervous system, including locomotor ataxia (known today as tabes dorsalis), which arises in the latter stages of syphilis.

In the early twentieth century, as modern medicine began to adopt a more rigorous scientific approach, interest in homeopathic remedies declined. The alleged curative powers of *Heloderma* received little attention for the remainder of the twentieth century. Because of its unorthodox methodology, homeopathic treatment using *Heloderma* has been largely dismissed in later accounts (Bogert and Martín del Campo 1956; Brown and Carmony 1991). With renewed interest in homeopathic remedies today, however, *Heloderma* has once again attracted the attention of some practitioners. One doctor of homeopathic medicine has developed a new, more complete, proving of *Heloderma* venom based on tests in 11 subjects (Rowe 2003). Heloderma has been recently used in homeopathic treatments of manic depression, aggression, hypertension, and multiple sclerosis (T. Rowe, pers. comm.). Because homeopathic remedies are often given at doses below levels that might be expected to have significant physiological effects, the mechanism of homeopathic cures (beyond the placebo effect) has so far eluded science. Like the indigenous folk remedies that preceded it, homeopathic medicine remains an obscure use of *Heloderma* venom for treating human disease. But as with most good folklore, an intriguing grain of truth may lie within.

In the 1980s, researchers discovered in the venom of helodermatid lizards some remarkable biologically active peptides that have strong physiological effects in mammals, including humans (chap. 3). Most of these compounds are similar in structure and action to vasoactive intestinal peptide (VIP), a mammalian hormone secreted by nerves throughout the gastrointestinal tract and other tissues. VIP is a powerful relaxant of smooth muscle and plays a role in the secretion of water and electrolytes by the small and large intestines. One of the VIP-like peptides discovered in *Heloderma* venom (named *helospectin;* see chap. 3) binds to VIP receptors in a number of human tissues in the gut, brain, lungs, and even the genitalia. In these tissues, helospectin may play a role in regulating secretory activities and local blood flow. Helospectin has been immunohistochemically located in the corpus cavernosum of the penis (Hauser-Kronberger et al. 1994), the clitoris (Hauser-Kronberger et al. 1999), and the human vagina, where it may play a role in the regulation of local blood flow and lubrication (Graf et al. 1995). Helodermin, another peptide discovered in the venom of *Heloderma* (and similar to helospectin), also binds to receptors in several human tissues including breast cancer cells (Raufmann 1996). It has even been shown to inhibit growth and multiplication of lung cancer cells (Maruno and Said 1993). These bioactive peptides from *Heloderma* venom are, in a sense, part of our physiology!

So it is a funny coincidence that ancient Mexican cultures thought extracts of *H. horridum* might "awaken the sexual appetite better than any known medicament" and that Boocock noted the effects of Gila Monster venom on erection and sexual performance (although he also noted dozens of other effects not unexpected in a person his age in the United States during the late nineteenth century). The powerful vasodilatory effects of some *Heloderma* venom constituents have not escaped the attention of modern researchers in pharmacology (chap. 3). Helospectin has been shown to relax tissue preparations of the corpus cavernosa, which mediates penile erection (Hedlund et al. 1995), to relax the vaginal wall of rabbits (Ziessen et al. 2002), and to possibly play a role in the female sexual response (Giuliano et al. 2002). In the human bronchi, helospectin also produces a potent relaxation response, which may open the airways of the lungs (Cardell and Cardell 2001).

We do not know why peptides from lizard venom reside in the most intimate places of our anatomy, or why they mimic our hormones. It is doubtful that extracts of *Heloderma* venom will become the next Viagra. But if good folklore contains a morsel of truth, the facts in this case are indeed more amazing than fiction.

And there are even more promising modern uses for constituents of *Heloderma* venom. The best known is Exendin-4, found naturally only in Gila Monster venom. Exendin-4 mimics another mammalian hormone, glucagon-like peptide, which mediates insulin release and glucose uptake from the blood after a meal (chap. 3). A synthetic version of exendin-4 is a leading candidate for treating adult-onset (Type II) diabetes, which accounts for most of the 17 million cases of diabetes in the United States. Prospects for this drug, called exentide, are so bright that pharmaceutical giant Eli Lilly & Company closed a $325 million deal in September 2002 with Amylin Pharmaceuticals for rights to develop and market this compound (Pollack 2002).

FOLKLORE AND SCIENCE

Scientists too have made their contributions to the folklore of the Helodermatidae. In a quirky juxtaposition of science and folklore, Bogert and Martín del Campo (1956) describe a fictional hybrid *Heloderma*-like reptile. The idea was contributed in part by Bogert's friend Lawrence Klauber, the renowned herpetologist and rattlesnake expert. Recall the famous Sherlock Holmes mystery "Adventure of the Speckled Band," in which poetic justice is served on Grimesby Roylott, who is killed by the same deadly reptile he set upon his victim. Upon discovering Roylott in the throngs of death, Holmes and Watson witness that "round his brow he had a peculiar yellow band, with brownish speckles." "The band! The speckled band!" whispered Holmes. Holmes identifies the deadly speckled band as "a swamp adder, the deadliest snake in India." But in a 1948 essay in *The Baker Street Journal* (an "Irregular Quarterly of Sherlockiana"), Lawrence Klauber argues how "the culprit could not, by any possibility, have been a snake at all." Klauber contends that Watson had misheard Holmes who had actually said "It is a samp-aderm, the deadliest skink in India" and that *samp-aderm* may be translated as "snake-Gila-Monster," a hybrid between a cobra and a *Heloderma* (Klauber 1948). "For we have here a sinister combination—a creature uniting the intelligence and agility of the lizard with the inimical disposition of the snake. It has fangs in the upper jaw inherited from one parent, and in the lower jaw from the other, and a venom incomparably strengthened by hybridization, thus assuring the almost instant demise of any victim" (Klauber 1948).

In their monograph on the Helodermatidae, Bogert and Martín del Campo (1956) expound on Klauber's wit in a description, complete with a drawing, of a new genus and species: *Sampoderma allergorhaihorhai*. The authors describe the new species as "Sausage shaped; identification is relatively simple if the following procedure is carried out. Touch the specimen employing the toe, finger, thumb, or, if preferred, the nose. If the result is instant death you may rest assured that you have correctly identified S. allergorhaihorhai." The prank, a result of Charles Bogert's lively imagination, was meant to poke fun at one of his stodgy colleagues at the American Museum of Natural History. It is not known whether Bogert's coauthor, Raphael Martín del Campo, was an accomplice in the hoax, but it remains another part of the rich folklore of the Helodermatidae.

HOW WE KNOW WHAT WE KNOW

The first major scientific treatment of the helodermatid lizards was an authoritative volume on the venom of *Heloderma* (Loeb et al. 1913). The book summarized detailed studies on the effects of the venom in a number of organisms and resolved the early debate over whether both species of helodermatid lizards were venomous (chap. 3). But it was not until 1956, when a broader synthesis of the Helodermatidae was put forth, that the importance of this unique family of lizards came to the attention of most biologists. This work, entitled "The Gila Monster and Its Allies," was a fortuitous synergy of the talents of two leading herpetologists, Charles M. Bogert and Raphael Martín del Campo, who produced one of the classics in twentieth-century herpetology. Their monograph provided the first comprehensive summary of the systematics, evolution, behavior, and folklore of both species of *Heloderma*. The work summarized the known distribution of the Helodermatidae and described two subspecies of *H. suspectum* and three subspecies of *H. horridum*. The publication of Bogert and Martín del Campo (1956) represented a major advance in our knowledge of the Helodermatidae and remains a cornerstone in our understanding of the biology of these unique lizards (Beck 1993). The monograph was reprinted in 1993 by the Society for the Study of Amphibians and Reptiles.

In recognizing the significant contribution that Bogert and Martín del Campo's work has made to our knowledge of helodermatid lizards, I have tried in this book to build on their foundation, rather than to repeat it. I'll begin here by offering a brief overview of some of the most noteworthy advances in the half century since Bogert and Martín del Campo (1956), and I'll outline some of the methods that have been used to make those discoveries. In the chapters that follow, I'll expound on these discoveries and their implications.

SOME EARLY FIELD STUDIES

When Bogert and Martín del Campo's monograph was published, very little was known about the ecology of helodermatid lizards; data on free-ranging animals were very limited. By necessity, the authors drew inferences from anecdotal accounts and analyses of preserved specimens. One of the earliest methods of monitoring helodermatid lizards in the field was to observe them at sites where they predictably return year after year. Among the first to publish such field observations was Ernest Tinkham, who described several Gila Monsters using rocky shelters along a conical knoll in southern Arizona (Tinkham 1971a). Tinkham reported that the lizards congregated at the site "in the fall of the year for hibernation" and that they appeared to select shelters on steep slopes with a southerly aspect, where they might bask on sunny winter days. He noted that by May most lizards had dispersed from the outcrop for their "summer peregrinations on the mesas."

During the 1950s and through the 1970s, H. L. Stahnke of Arizona State University took a great interest in *H. suspectum* and conducted a number of laboratory and field observations on these lizards. Although many of his field studies were never published, his observations on diet were important in showing that Gila Monsters may feed on large prey items in nature (Stahnke 1950, 1952). Stahnke was also a tireless champion for establishing legislation to protect populations of *H. suspectum* from wanton killing and commercial exploitation (Brown and Carmony 1991). Through his efforts, as well as those of C. H. Lowe (discussed below), *H. suspectum* in Arizona became the first venomous reptile to receive legal protection (Grant 1952).

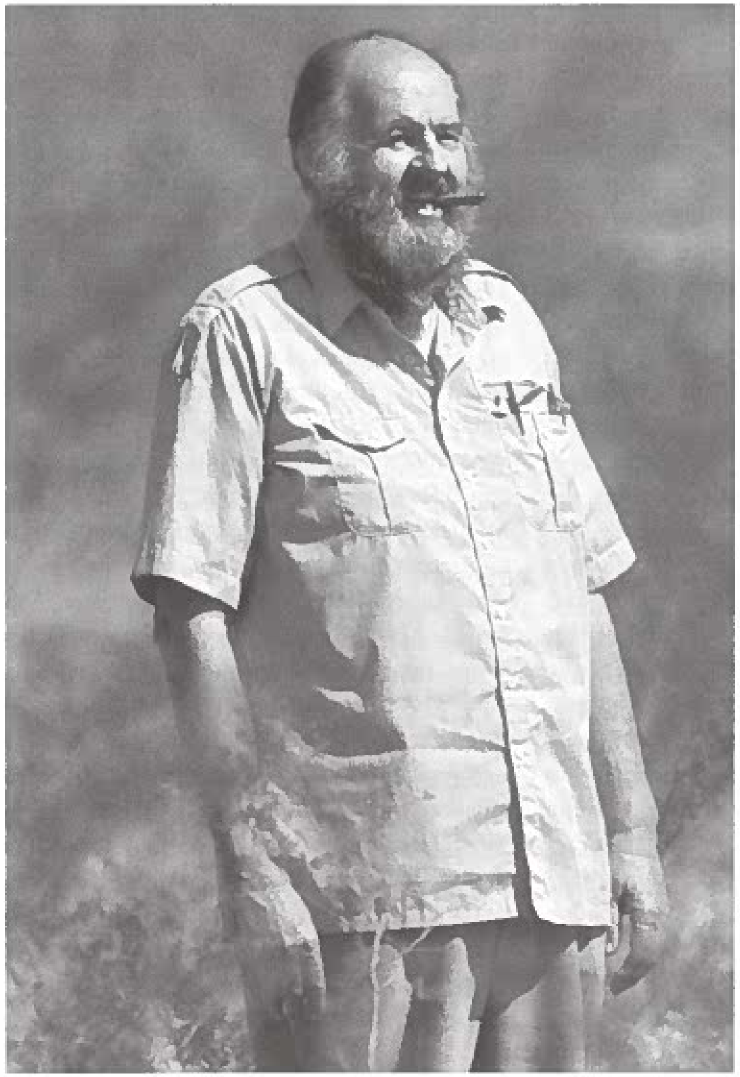


FIGURE 2. Charles H. Lowe (1920–2002), one of the preeminent desert naturalists of the twentieth century, was also one of the foremost students of helodermatid lizards.

Among the greatest students of helodermatid lizards in the twentieth century was the late eminent desert ecologist Charles H. Lowe (fig. 2). In his early 20s, he accompanied C. M. Bogert and J. A. Oliver on one of the earliest intensive collecting expeditions into Sonora, Mexico (Bogert and Oliver 1945). Not long after arriving at the University of Arizona as a young assistant professor in 1949, Lowe became established as a leader in ecological research in the Sonoran Desert region, a role that would span five decades. Perhaps Lowe is best known as a major catalyst in untangling the taxonomic difficulties and mystery of parthenogenesis in whiptail lizards (genus *Cnemidophorus;* e.g., Lowe and Zweifel 1952; Lowe 1955; Lowe and Wright 1966; Wright and Lowe 1967, 1968; Lowe 1993), or for his classic work with W. Steenbergh on saguaro cacti (Steenbergh and Lowe 1969, 1971, 1977, and 1983), or for the well-known map on the biotic communities of the Southwest that he produced with D. Brown (Lowe 1968; Brown and Lowe 1974, 1980; Brown et al. 1979; Lowe and Brown 1982). His landmark book on the vertebrates of Arizona and their habitats (Lowe 1964) remains useful and in high demand today. Throughout all of these contributions, Lowe maintained a passionate interest in helodermatid lizards. He made many field observations and conducted many experiments on physiology, behavior, and growth (Brown and Lowe 1954, 1955; Lowe et al. 1967, 1971, 1986; Lardner 1969; John-Alder et al. 1983; Beck and Lowe 1991, 1994; Beck et al. 1995; Goldberg and Lowe 1997; Schwalbe and Lowe 2000). A tireless advocate of field studies, Lowe, along with his students, spent many days in the field observing Gila Monsters. He inspired his students to develop novel field methods, such as a tail spool for trailing the movements of Gila Monsters in nature (Heath 1961). He monitored several winter hibernacula similar to those described by Tinkham (1971a) (chap. 6; Martin and Lowe 2001). When Brent Martin arrived in Tucson as an enthusiastic field student in the 1970s, Lowe helped him establish a research protocol for several sites near Tucson, Arizona, where Gila Monsters overwinter on rocky slopes in relative proximity to one another. Observations of the Gila Monsters returning to those overwintering locations continued throughout the 1970s, 1980s, and 1990s and have become the longest running field study ever conducted on helodermatid lizards.

While at the University of Arizona, Lowe built one of the world's best collections of southwestern amphibians and reptiles, including the largest collection of helodermatid lizard specimens in the world. He was a strong player in helping the Arizona-Sonora Desert Museum become established as a premier educational and research organization during its formative years, and he helped keepers there become among the first to successfully breed *Heloderma* in captivity. In 1986, Lowe published a definitive book on the venomous reptiles of Arizona with C. Schwalbe and T. Johnson (Lowe et al. 1986) that synthesized much of what he had learned from his field observations of *Heloderma* over the years. Never wanting to publish results until he felt he had the whole story, Lowe held onto many of his data for decades until a tragic fire in 1994 destroyed his home and many of his records. The legacy of Lowe also lives in the accomplishments of his students and in the passion for fieldwork that he infused in all of us who worked with him. Much of the information presented in this book would never have seen the light of day had it not been for Lowe. Some of the data that he and Brent Martin collected appear in chapter 6 of this book. Charles H. Lowe died in Tucson, Arizona, in September, 2002, at 82. Much of the work he conducted on *Heloderma* with Brent Martin remains to be published. Stay tuned.

Another important contributor to early studies of *Heloderma*, particularly *H. horridum*, was Miguel Álvarez del Toro, one of the preeminent naturalists of Latin America during the twentieth century (Flores-Villela and Hodges 1999). In 1942, Don Miguel, as he was known by his peers, established a zoological park in Tuxtla Gutiérrez, Chiapas, Mexico that became recognized as one of the finest living museums in the neotropics. He established and maintained a small colony of *H. horridum* at his zoo. Don Miguel made a number of observations on the natural history and behavior of *H. horridum*, many of which were summarized in his landmark book *Los Reptiles de Chiapas* (Álvarez del Toro 1960, 1972, 1982). He was the first to describe the likely reproductive cycle (based on field observations) of *H. horridum* and, with his students and staff, helped interpret the spectacular combat rituals performed by male *H. horridum* (Ramírez-Velázquez and Guichard-Romero 1989). A new subspecies of *H. horridum* (*H. h. alvarezi*) was named in his honor by Bogert and Martín del Campo (1956).

One of the early researchers to undertake a field study of the Gila Monster was Eric Coombs who, between 1975 and 1977, monitored a population near St. George, Utah (Coombs 1977). Coombs marked and measured 15 Gila Monsters and employed some novel techniques to follow trackways and observe field behaviors. He recorded some of the earliest measurements of body temperatures and estimates of home ranges of Gila Monsters active in nature. Coombs' work laid the foundation for some of my subsequent fieldwork on *H. suspectum* in Utah (Beck 1985b, 1986, and 1990).

TECHNIQUES AND NEW DIRECTIONS

Because both species of *Heloderma* offer observers only fleeting glimpses of their behavior in nature, most information on their natural history remained primarily anecdotal until well into the 1980s. Aside from watching individuals that return to rocky knolls for overwintering, how does one actually investigate the ecology of a lizard that spends over 95% of its time hidden in shelters? Some investigators have simply followed Gila Monsters from a distance, observing individuals as they forage (Jones 1983). However, such an option might be possible only under extraordinary conditions. Another useful method is to follow tracks. When Gila Monsters walk across sandy habitats they leave conspicuous and readily identifiable trackways that may remain for several days (see plate 21). Much information can be gleaned by examining these trackways. Tracks that are less than a few hours old can be recognized by indentations left in the sand from the small scales of the feet and toes. Individual lizards that have lost parts of toes, or that have been toe-clipped by the investigator, are also readily identified by their trackways (fig. 3). (Note, however, that researchers today use less invasive techniques, such as recording unique features of an individual's dorsal pattern, for identifying recaptured lizards. Toe clipping is no longer encouraged and is seldom used to identify individual helodermatid lizards.) The investigator can follow trackways into burrows, across dunes, and even into foraging sites, thereby gaining valuable information on the timing and distance of certain aboveground forays. At one of my Utah study sites, I followed hundreds of such trackways and encountered several new Gila Monsters (Beck 1986, 1990). One June morning I followed a set of tracks that ended at a Desert Tortoise nest being excavated and devoured by a Gila Monster (chap. 7). Sand tracking has been used successfully at sites in Utah and Nevada (Coombs 1977; Beck 1990; B. McGurty, pers. comm.; Gienger 2003), but it has obvious limitations. Trackways are nearly impossible to see in the majority of habitats where Gila Monsters are active, such as gravelly slopes, wash bottoms, and rocky areas of the Sonoran Desert. Relying solely on information from sandy habitats may give the false impression that Gila Monsters are more active in these areas than in other habitats and may yield a biased perspective on foraging pathways and activity patterns.

The advent of radiotelemetry opened a new window of discovery into the ecology of helodermatid lizards (as well as many other secretive reptiles). The first researchers to use radiotelemetry to track Gila Monsters were Schwartzmann and Ohmart (1976), who tested temperature-sensitive radio transmitters in two lizards in south-central Arizona. Their preliminary study was expanded by Porzer (1981), who monitored body temperatures and activity patterns of four radio-equipped Gila Monsters in Queen Creek, Pinal County, Arizona. Porzer was the first to quantify the amount of time Gila Monsters spend resting and active in nature, and she found that 95.6% of their time was spent in belowground retreats.

The pioneering field studies of Coombs (1977) and Porzer (1981) had just been completed when I began my fieldwork on *H. suspectum* in 1982. In the 1980s and 1990s, I used radiotelemetry in three separate studies on helodermatid lizards in Utah; Jalisco, Mexico; and New Mexico (see Beck 1990; Beck and Lowe 1991; Beck and Ramírez-Bautista 1991; and Beck and Jennings 2003). An advantage of radiotelemetry is that one can pinpoint the location of a subject at any time and thereby gain valuable information on home range, activity patterns, and habitat use. Temperature-sensing implantable radiotransmitters also allow investigators to monitor body temperatures. A temperature-sensing radiotransmitter emits beeps whereby the pulse interval (time period between beeps) decreases predictably as temperature increases. Before they are surgically

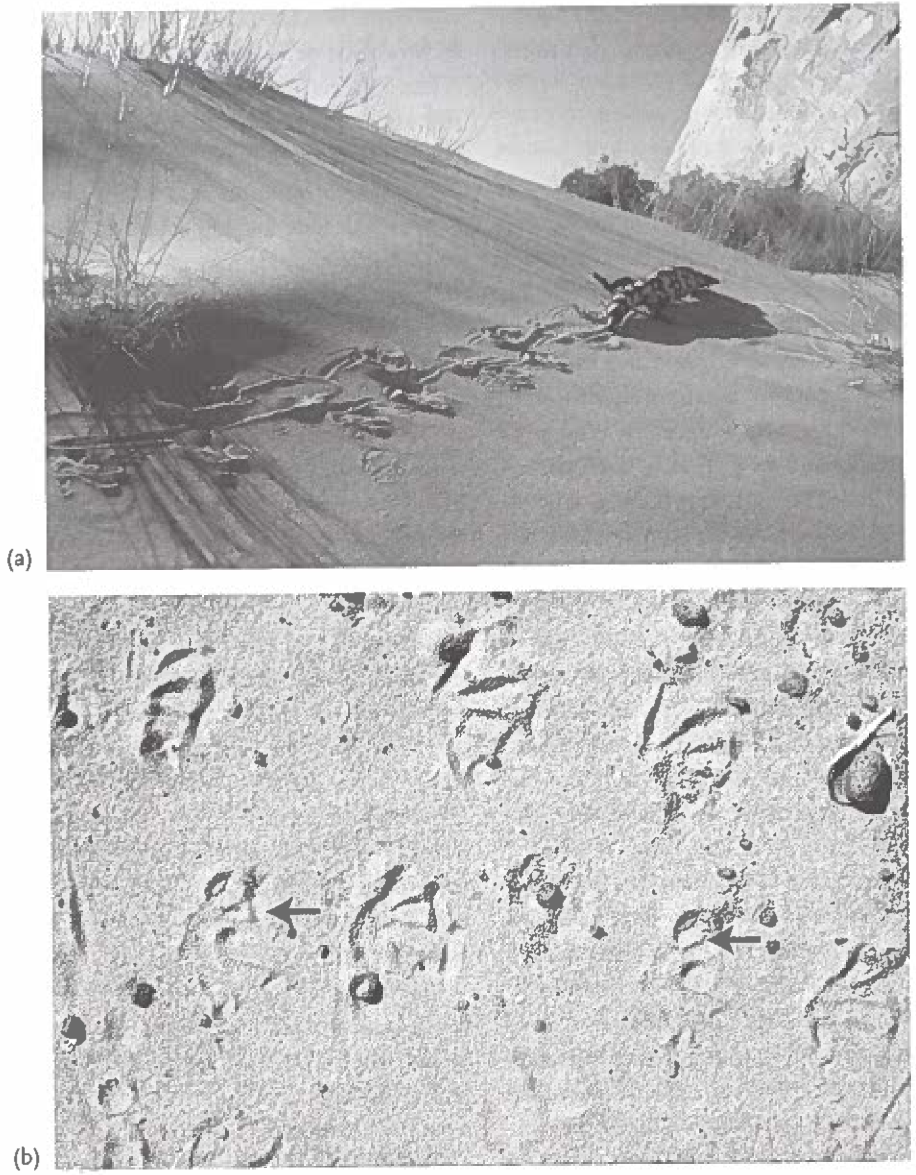


FIGURE 3. (a) As they travel across sandy environments, helodermatid lizards leave conspicuous trackways. (b) Individual Gila Monsters can sometimes be identified by their tracks. Note the indentation left by a clipped toe on the right front foot (at arrows) that identifies this trackway as belonging to lizard no. 8 (photo by Dan Beck).

implanted into the lizards, the radios are carefully calibrated in a water bath at the same range of temperatures that the lizard might experience in nature over the course of a year. When radiotracking Gila Monsters and Beaded Lizards at my study sites, I would frequently check the pulse intervals from the radios to determine whether lizard body temperatures were relatively constant or fluctuating. When lizards remained in shelters their body temperatures would typically fluctuate very little over time. But as a lizard leaves the relatively stable thermal environment of its shelter, its body temperature begins to fluctuate (chap. 4). It becomes relatively easy to pinpoint exactly when lizards emerge from shelters by noting these nuances in body temperatures over time.

Radiotelemetry allows investigators to accurately monitor movements, activity patterns, and habitat use. Microhabitats that are visited by lizards can be characterized and compared with other microhabitats that appear to be avoided. In this way, habitat features can be identified that are important to helodermatid lizards (Beck and Lowe 1991; Beck and Jennings 2003). In our New Mexico study, we used radiotelemetry to identify hundreds of shelters used by Gila Monsters. We then placed miniature dataloggers that continuously recorded temperature and humidity within a sample of those shelters. We found that Gila Monsters select shelters based on certain physical features (such as rockiness, directional aspect of the entrance, and humidity), that they return year after year to the same shelters, and that shelters are an important part of the social structure of the population (Beck and Jennings 2003; chap. 5).

Using radiotelemetry to monitor temperature requires bulky receivers and antennas. But now investigators can generate a continuous record of body temperatures by surgically implanted miniature dataloggers inside the body cavity. After recording data for a specific period, the dataloggers can be removed and the data downloaded onto a computer. One model of datalogger (iButton, Dallas Semiconductor, Dallas, TX) that was developed to monitor the temperature of perishable foods during shipment is about the size of five dimes stacked on top of one another. Miniature iButton dataloggers are being used to monitor body temperatures and activity periods of Gila Monsters in the Sonoran Desert north of Tucson, Arizona by Dale DeNardo and his students at Arizona State University (Mattlin et al. 2003; chap. 5).

In recent years, the number of researchers using radiotelemetry to track Gila Monsters has increased considerably. Sullivan et al. (2004) monitored the fate of 25 Gila Monsters reported as "nuisances" by human residents in metropolitan Phoenix, Arizona. Their study revealed some important findings about the fate of Gila Monsters that are relocated in suburban areas (chap. 9).

In the Mohave Desert of Southern Nevada, C.M. Gienger (of the University of Nevada, Reno) began radiotracking several Gila Monsters in 2001 to investigate home range, activity patterns, thermal biology, and water balance (Gienger 2003). He also used geographical information system (GIS) technology to develop a habitat model for the Gila Monster in southern Nevada (see chap. 9). His work continues (with C.R. Tracy of the University of Nevada, Reno and K. Nagy of UCLA), in an effort to investigate water and energy balance in both the field and the laboratory.

In the Sonoran Desert of southern Arizona, at least two ongoing studies are using radiotelemetry to investigate the biology of Gila Monsters in nature. In a long-term study aimed at investigating habitat use, physiology, and behavior of *H. suspectum*, R. Repp of Tucson, Arizona and G. Schuett of the University of Georgia and Zoo Atlanta began radiotracking several Gila Monsters in 2001 at a site north of Tucson. They have so far compiled numerous observations of refuge site fidelity, activity patterns, behavior, and diet. Gila Monsters are seen returning to the same sites, raiding quail nests, and pairing within shelters.

At a site nearby, D. DeNardo and his colleagues at Arizona State University continue radiotracking several Gila Monsters in a study of activity patterns, thermal biology, and physiology. Their fieldwork is showing that Sonoran Desert Gila Monsters show considerable nocturnal activity during the summer monsoon season (chap. 5). These researchers are also conducting laboratory investigations of evaporative water loss, the possible role of the urinary bladder as a water storage organ, and other physiological variables. DeNardo et al. (2004) fashioned a diaper for differentiating cloacal from cutaneous evaporative water loss. Their findings are validating earlier indications (Lowe et al. 1986) that Gila Monsters have "leaky skins." In a surprising result, DeNardo et al. (2004) discovered that evaporative water loss from the cloaca increases dramatically at body temperatures above 35°C, so much so that it serves to reduce body temperature within this stressful zone by as much as 2°C (chap. 4).

As DeNardo's work demonstrates, laboratory techniques have been an important complement to field studies of helodermatid lizards since Bogert and Martín del Campo (1956). In an earlier study, Lardner (1969) used large running wheels in the laboratory to investigate the rhythmicity of activity by Gila Monsters. He found that locomotory patterns tended to be repeated every 22.5 to 25.3 hours and that this periodicity was affected by temperature, light, and food deprivation. About 15 days after food deprivation, locomotory activity became more sporadic and frequent (Lardner 1969). Motorized treadmills have been used in a laboratory setting to measure sprint speed and endurance in helodermatid lizards (Beck et al. 1995). Beaded Lizards and Gila Monsters have been outfitted with masks that direct exhaled air through an oxygen analyzer for use while they are walking on treadmills. Rates of oxygen consumption can then be calculated, which enable researchers to determine activity metabolism and the cost of locomotion (John-Alder et al. 1983; Beck 1991; Beck et al. 1995; chap. 4). Helodermatid lizards have also been placed in metabolic chambers in the laboratory where oxygen consumption rates are measured at various temperatures while the lizards are at rest. These studies have shown that helodermatid lizards have very low resting metabolic rates (Beck and Lowe 1994; chap. 4). Researchers have also investigated behavior and chemoreception of helodermatid lizards in the laboratory by observing tongue-flicking responses to a variety of chemical cues (Cooper 1989; Cooper et al. 1994; Cooper and Arnett 1995, 2001; Garrett et al. 1996). The mechanics of egg eating by *H. horridum* has been analyzed in the laboratory with X-ray video imaging (Herrel et al. 1997; chap. 7).

New technologies are not the only means by which our understanding of the helodermatid lizards has been enhanced in the past 50 years. The same techniques employed by Bogert and Martín del Campo (1956)—careful examination of specimens captured from the field—have been equally important and are still very useful today. In 1988, a new subspecies of Beaded Lizard (*H. h. charlesbogerti*) was described in this manner based on careful examination of specimens from eastern Guatemala (Campbell and Vannini 1988; chap. 2). An analysis of preserved specimens has yielded valuable information on population ecology (chap. 6), sexual dimorphism (Gienger and Beck unpubl. ms.), and food habits (chap. 7). An analysis by Herrel and DeVree (1999) of the cervical musculature of preserved *Heloderma* specimens has been used to investigate the important evolutionary step of using the jaws (rather than the tongue) to take prey into the mouth (chap. 7). And while the potential knowledge contained in preserved specimens may be huge, basic field observations of natural history will forever remain invaluable.

Some of the most exciting advances occur when solid field observations are coupled with new technologies. In a final example, Douglas et al. (2003) examined the molecular diversity within the Helodermatidae by sequencing two mtDNA genes (ATPase 8 and 6) from both species sampled across their distribution in the United States, Mexico, and Guatemala. As discussed in chapter 2, their results suggest that three of the subspecies of *H. horridum* might actually be separate species. In addition, the preliminary analyses of Douglas et al. (2003) provide little basis for recognizing either of the two *H. suspectum* subspecies (chap. 2).

The Helodermatidae has a rich legacy—from both sociological and biological perspectives. It even seems plausible that the Helodermatidae may change the way we view lizards, culturally, ecologically, and evolutionary. But as with many species today, the fate of the Helodermatidae is uncertain. In the nearly 50 years since Bogert and Martín del Campo's seminal work was published, the earth's human population has more than doubled from 2.8 billion to over 6.2 billion people. Desert and tropical dry forest habitats have disappeared at an alarming rate (chap. 9), and many species have gone extinct as a result of humankind's activities. We cannot even estimate the true number of species that have disappeared because many extinctions likely occur before biologists even know such species exist (Wilson 1993). Some populations of helodermatid lizards are in danger of extirpation (chap. 9). With only two (perhaps four) species in one genus, the Helodermatidae seems almost a relic of a bygone time, especially when compared with their closest living relative, *Varanus*, which contains around 50 species (Pianka and King 2004). As the twenty-first century gets under way, we have an opportunity—indeed a responsibility—to take what we know and use it to sensibly manage what remains of the earth's magnificent heritage of biodiversity. I hope this book will help give researchers, educators, managers, and citizens both the inspiration and the ammunition to do this for our only venomous lizards.

CHAPTER 2

Evolution, Distribution, and Systematics

THE HELODERMATIDAE contains only one extant genus, but throughout their evolutionary history at least six other genera of helodermatid lizards have come and gone. Our knowledge of the evolution and systematics of these lizards has recently received a boost from both advances in methodology and the hard work of field paleontologists. Discoveries of several exciting fossils in North America and Asia have revealed details about the ancestors of *Heloderma*, and the advent of sophisticated new techniques for analyzing phylogenetic relationships has allowed us to better understand the evolutionary relationships among these fossils and extant lizards. These advances show that the Helodermatidae has a rich and diverse evolutionary history that extends across Europe, Asia, and North America. The helodermatid clan, a well-supported lizard clade recently named the Monstersauria, dates back 100 million years to within the age of dinosaurs. These lizards have undergone relatively little gross morphological change over this time, prompting many to regard them as living fossils.

In this chapter, I'll summarize the taxonomy and distribution of recent helodermatid lizards. I'll review what is known of their fossil record and summarize their phylogenetic relationships with other lizards and snakes. In addition, I'll discuss some evolutionary scenarios and interpretations of the fossil record of this ancient group of saurians.

CONTEMPORARY HELODERMATID LIZARDS

DESCRIPTION

Helodermatid lizards can be recognized by the presence of rounded, beadlike osteoderms on dorsal surfaces of the head, limbs, body, and tail (plate 1). Robust skull architecture, large jaw muscles, and venom glands in the lower jaw give the head a bulky appearance (fig. 4). The black snout is bluntly rounded. The eyes are relatively small and somewhat protuberant, covered by movable eyelids. The teeth are long and recurved; some are modified with venom-conducting grooves on both the anterior and posterior surfaces (see chap. 3). Helodermatid lizards have thick tongues that are forked distally and either pink (in *H. horridum*) or black (in *H. suspectum*). The limbs are relatively short, the fourth toe of the hind foot is not enlarged, and all of the digits possess strong, recurved claws. Fat reserves are stored in the tail, which can be thick in well-fed individuals but is often quite thin in wild-caught lizards. The tail does not break easily and does not regenerate if severed. The hemipenis is small and undivided with flounced ornamentation that extends to the apex (Camp 1923; Campbell and Lamar 2004). The reader is referred to Bogert and Martín del Campo (1956) and Campbell and Lamar (2004) for a more detailed discussion of morphological characteristics of the Helodermatidae and to chapter 6 for a discussion of body size in *Heloderma*.

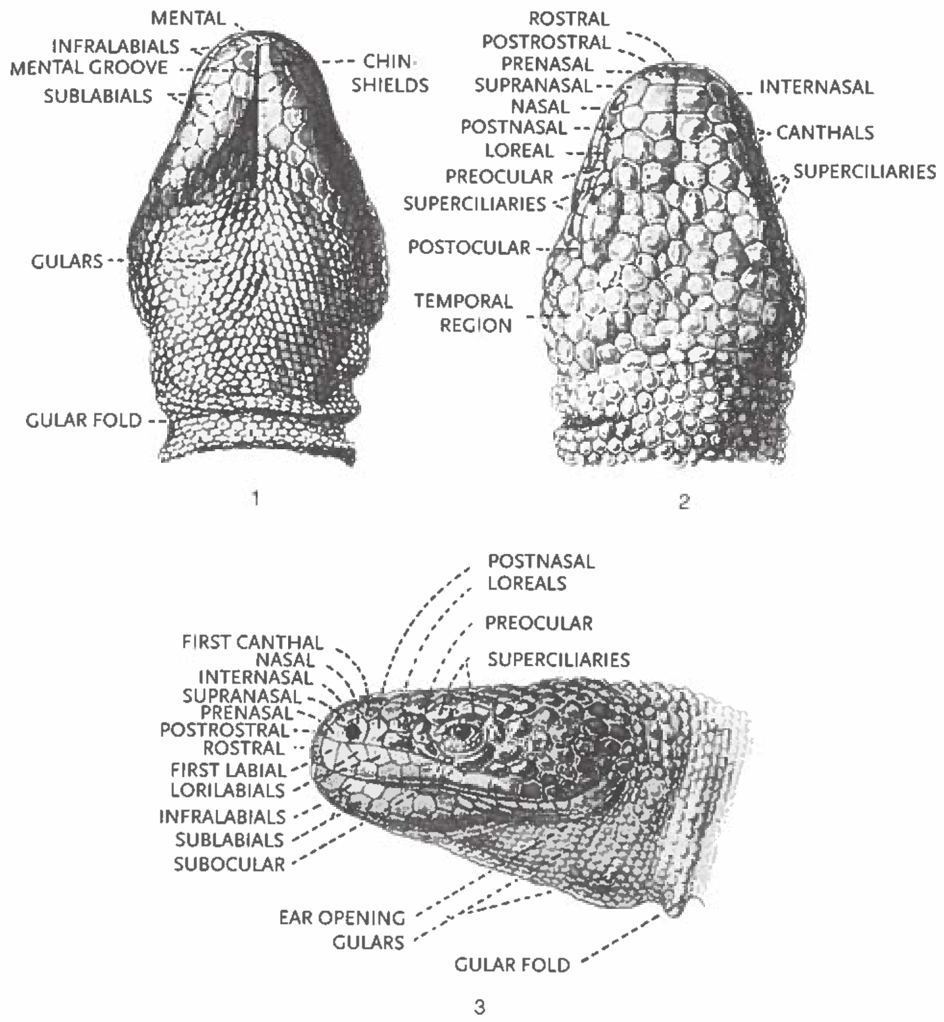


FIGURE 4. Head of *Heloderma horridum* showing general form and scutellation (from Bogert and Martín del Campo 1956; used with permission from the Bulletin of the American Museum of Natural History, vol. 109).

HELODERMA HORRIDUM WIEGMANN 1829

Heloderma horridum is a longer, lankier, more arboreal lizard than is *H. suspectum*. In nature, adults reach a snout-to-vent length (SVL) of 330–480 mm, an overall length of 570–860 mm, and a mean adult body mass of around 800 g. Individuals may rarely approach 1 m in overall length and weigh over 2 kg (see chap. 6). The two species are readily distinguished from each other by the proportionately longer tail of *H. horridum*, which comprises at least 60% of the SVL. In *H. suspectum* the tail is no more than 56% as long as the SVL (table 1). *Heloderma suspectum* typically have two conspicuously enlarged preanal scales (fig. 5f), whereas *H. horridum* normally have no enlarged preanal scales, although some individuals from eastern Guatemala are an exception (Campbell and Vannini 1988). In addition, *H. horridum* has two pairs of infralabials that are in contact with

TABLE 1

Selected Characteristics That Serve to Distinguish the Two Species of Helodermatid Lizards

	HELODERMA HORRIDUM	*HELODERMA SUSPECTUM*
Adult size (total length)	Commonly over 600 mm; up to nearly 1.0 m	Up to 570 mm
Ratio of tail length to snout-to-vent length	0.60–0.90	0.36–0.56
Scales from vent to tail tip	73–87	48–62
No. of caudal vertebrae	40	25–28
No. of subcaudal scales	73–87	48–62
Enlarged preanal scales	0 (usually)	2
No. of infralabials contacting anterior chin-shields	2	1
Color of tongue	Pink	Black

the chin shields, whereas *H. suspectum* has but one (fig. 5c–e). Male *H. horridum* also tend to have proportionately longer tails than do females (Gienger and Beck unpubl. ms.).

The binomial *Trachyderma horridum* was first applied to the type specimen (Wiegmann 1829). Realizing that *Trachyderma* was preoccupied, Wiegmann proposed *Heloderma* for the genus (from Greek *helos*, meaning "studded" and *derma* meaning "skin," in reference to the bony osteoderms).

The distribution of *H. horridum* extends over 13 degrees of latitude, or 1600 miles from southern Sonora, Mexico, to eastern Guatemala, from near sea level to 1600 m (fig. 6). Thus it should be no surprise that a great deal of clinal variation occurs among the populations inhabiting this extensive region. Bogert and Martín del Campo (1956) recognized this when they described three subspecies of *H. horridum: H. h. exasperatum* extending from Sonora to Sinaloa, *H. h. horridum* from southern Sinaloa to Chiapas, and *H. h. alvarezi* from Chiapas (and later, southwestern Guatemala; Stuart 1963). What at first appeared as a disjunct distribution of these three subspecies (Bogert and Martín del Campo 1956) is now known to be more or less continuous from southern Sonora to western Guatemala (Campbell and Vannini 1988). A hiatus in the distribution of *H. horridum* may occur in southeastern Chiapas and southwestern Guatemala (Campbell and Lamar 1989, 2004). A fourth subspecies, *H. h. charlesbogerti*, was described from eastern Guatemala by Campbell and Vannini (1988).

A recent genetic analysis of the Helodermatidae (Douglas et al. 2003) shows that variation among the subspecies of *H. horridum* is even greater than previously recognized. These researchers examined the molecular diversity within the Helodermatidae by sequencing 840 base pairs of two mtDNA genes (ATPase 8 and 6) from 50 individual *H. horridum* and 87 individual *H. suspectum* sampled across their respective ranges. The analysis was rooted with the outgroup Anguidae (genus *Elgaria*) and explored using Bayesian analysis (Douglas et al. 2003). *H. horridum* showed approximately 20% divergence from *H. suspectum*, and the genus *Heloderma* showed 34%–35% sequence divergence from the outgroup *Elgaria* (table 2). Northernmost populations of *H. h. exasperatum* from near Alamos, Sonora, showed 6.1% divergence from *H. h. horridum* from Jalisco, 9.6% divergence from *H. h. alvarezi* from Chiapas, and 10.1% base sequence divergence from the southernmost populations of *H. h. charlesbogerti* from eastern Guatemala (Douglas et al. 2003; table 2). These differences in mtDNA base sequences are well beyond the range that normally differentiates subspecies, suggesting that there might actually be three species of Beaded Lizards: *H exasperatum*, *H. horridum*, and *H. alvarezi* (Douglas et al. 2003). Pending review of the changes proposed by Douglas et al. (2003), however, I'll use the historical taxonomy in the following accounts.

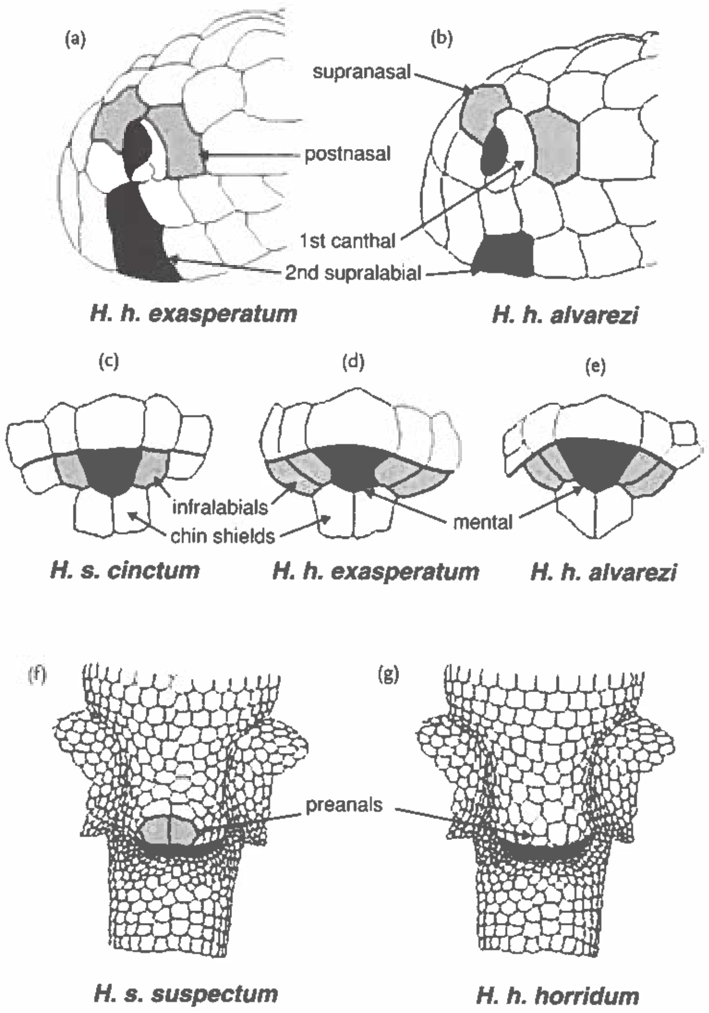


FIGURE 5. Scale characteristics used by Bogert and Martín del Campo (1956) to describe differences among species and subspecies of helodermatid lizards (used with permission from Campbell and Lamar 2004).

HELODERMA HORRIDUM EXASPERATUM BOGERT AND MARTÍN DEL CAMPO 1956

RIO FUERTE BEADED LIZARD OR ESCORPIÓN DEL RÍO FUERTE

The northernmost subspecies of Beaded Lizard, *Heloderma horridum exasperatum*, was described from a type specimen near the village of Guirocoba, Sonora, Mexico (Bogert and Martín del Campo 1956). It occurs primarily in the foothills of the Sierra Madre Occidental within the drainage basins of the Rio Mayo and Rio Fuerte of southern Sonora and northern Sinaloa (fig. 6). Within this region, its distribution closely matches fingers of tropical deciduous forest that extend north and east from Alamos, Sonora, although *H. exasperatum* occasionally ventures into pine–oak woodlands at higher elevations and tropical thornscrub at lower elevations (Ottley 1981a; Schwalbe and Lowe 2000; chap. 5). Bogert and Martín del Campo (1956) thought it "virtually certain" that the subspecies would be found in the barrancas of western Chihuahua.

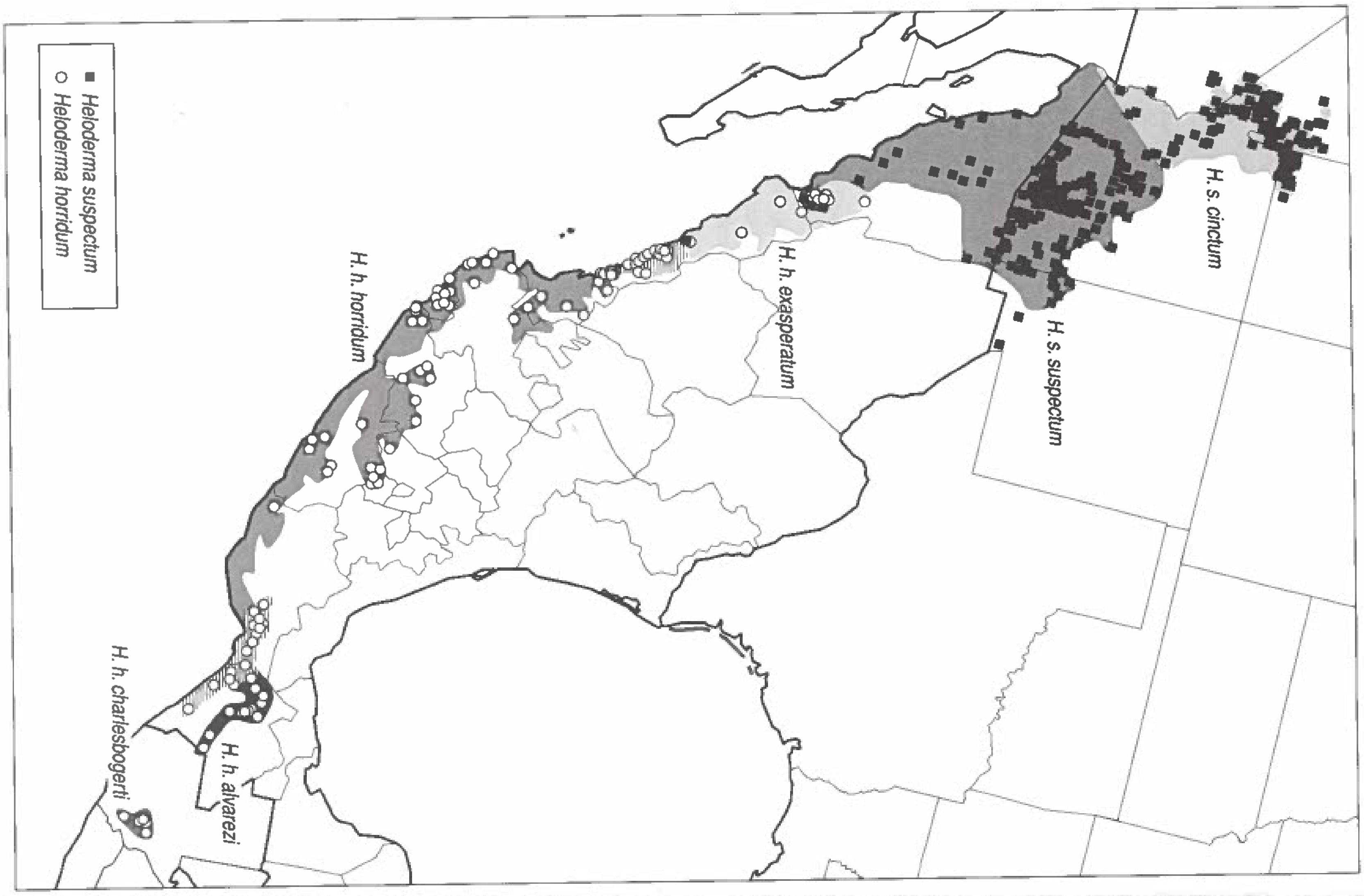


FIGURE 6. Range map of the Helodermatidae. Regions with horizontal stippling indicate integrated zones between subspecies.

TABLE 2

Percentage Sequence Divergence Found among Clades of Helodermatid Lizards and Their Outgroup (Elgaria)

	H. H. ALVAREZI	*H. H. CHARLESBOGERTI*	*H. H. HORRIDUM*	*H. H. EXASPERATUM*	*H. SUSPECTUM*	*H. S. CINCTUM* (NEVADA)	*ELGARIA*
H. h. alvarezi	—	1.0%	5.2%	9.6%	20.0%	21.0%	35.0%
H. h. charlesbogerti	0.003	—	6.0%	10.1%	20.6%	21.5%	35.8%
H. h. horridum	0.006	0.007	—	6.1%	18.2%	19.0%	33.6%
H. h. exasperatum	0.01	0.011	0.007	—	20.3%	21.3%	35.7%
H. suspectum	0.013	0.013	0.012	0.013	—	0.5%	34.0%
H. s. cinctum (Nevada)	0.013	0.013	0.012	0.013	0.001	—	34.6%
Elgaria	0.016	0.016	0.016	0.016	0.016	0.016	—

NOTE: Based on mtDNA genes ATPase 8 and 6 (Douglas et al., unpublished data). Upper triangle of matrix represents pair-wise average sequence divergence (p-distance) among clades corrected for within-clade variance, whereas the lower triangle contains pair-wise estimates of standard error. Calculations were performed using Mega version 2.1 (Kumar et al. 2001).

Fingers of tropical dry forest certainly extend into Chihuahua (Brown and Lowe 1980; Van Devender et al. 2000), but the nearest valid specimen of *H. h. exasperatum* to date is from Moras, Sonora (Ottley 1981a), 33 km west of the Chihuahua border. Much of its former habitat in Sinaloa has been converted to agriculture, but remnant populations likely survive wherever tropical dry forest habitats remain intact. In a few localities (e.g., south of Alamos near the village of San Vicente and west of Alamos where thornscrub and tropical dry forest habitats interdigitate), both *H. exasperatum* and *H. suspectum* may be found together (Ottley 1981b; personal observation). Knowledgeable villagers near Cerro Pelón have told me that they have observed Gila Monsters (escorpión pintado) on a south-facing slope consisting of thornscrub/ desert scrub vegetation and Beaded Lizards (escorpión negro) on the opposite, north-facing slope consisting of deciduous forest vegetation. However, differences in habitat preferences likely prevent the two species from occupying the same microhabitats. In tropical dry forest habitats north of Mazatlan, Sinaloa, *H. h. exasperatum* likely intergrades with *H. h. horridum* (fig. 6).

In the sample examined by Bogert and Martín del Campo (1956), *H. h. exasperatum* differed from other Beaded Lizards by having the supranasal scale always in contact with the postnasal, rather than separated by the first canthal (fig. 5a, b). *H. h. exasperatum* also had more scales (8 rather than 6 or 7) on top of the head between the superciliaries, and a shield-shaped mental scute (fig. 5d). However, these differences in head scalation, along with others discussed by Bogert and Martín del Campo (1956), vary considerably among the Beaded Lizards and may not always be reliable in diagnosing different subspecies (Hardy and McDiarmid 1969; Johnson and Ivanyi 2001).

A more predictable trait that sets *H. h. exasperatum* apart from other Beaded Lizards may be its dorsal pattern, which tends to be more speckled with yellow, especially on the tail, than that of other Beaded Lizards (plate 13). Juveniles tend to be dark, with distinctive spotting and tail banding that breaks up with age.

HELODERMA HORRIDUM HORRIDUM WIEGMANN 1829
THE MEXICAN BEADED LIZARD, ESCORPIÓN, OR ACALTETEPÓN

The nominate subspecies of Mexican Beaded Lizard can be found in tropical dry forest habitats from southern Sinaloa through Nayarit, Jalisco, Colima, Michoacán, Mexico, Guerrero, Morelos, and Oaxaca, from near sea level to 1500 m elevation (fig. 6). Although there is some uncertainty about the actual location of the type specimen of *H. horridum*, it apparently came from the state of Morelos, Mexico, near the town of Huajintlán (Bogert and Martín del Campo 1956).

H. h. horridum shows the greatest latitudinal range of all the Beaded Lizards and also the greatest variability. In the north, populations of *H. h. horridum* tend to have a shield-shaped mental scale with distinct lateral indentations that become less conspicuous in the south (Bogert and Martín del Campo 1956; fig. 5d). The dorsal patterns of *H. h. horridum* consist of distinctive yellowish dots and blotches on a black or brown background. These patterns are extremely variable, even within a single population (plate 13), and they change with age. Juveniles have yellowish dots, bars, or spots on a dark background and distinctive yellow tail bands. As individuals mature, lighter regions break up, additional yellowish spots appear on the dark background, and dark color invades the solid-yellow tail bands. Adult *H. h. horridum* generally do not have as many fine yellowish speckles, especially on the tail, as do individuals of *H. h. exasperatum* (plate 13). Bogert and Martín del Campo (1956) described an adult *H. h. horridum* specimen from Chilpancingo, Guerrero, that was almost uniformly black. In eastern Oaxaca some adults may show only faint yellowish markings on a dark background. In this region, between the Isthmus of Tehuantepec and Cintalapa, Chiapas, *H. h. horridum* appears to integrade with *H. h. alvarezi* (Álvarez del Toro 1982; Campbell and Vannini 1988).

HELODERMA HORRIDUM ALVAREZI BOGERT AND MARTÍN DEL CAMPO 1956
RÍO GRIJALVA, CHIAPAN, OR BLACK BEADED LIZARD, OR ESCORPÍON NEGRO

The Chiapan Beaded Lizard was named in honor of Don Miguel Álvarez del Toro (see chap. 1) who also collected the type specimen near Tuxtla Gutiérrez, Chiapas, Mexico. Additional specimens collected by Stuart (1963) extended the range of *H. h. alvarezi* into southwestern Guatemala. *H. h. alvarezi* is now known to inhabit the Río Grijalva Valley through central Chiapas into the Río Lagartero Depression of western Guatemala (Bogert and Martín del Campo 1956; Stuart 1963; Álvarez del Toro 1982; Campbell and Lamar 1989, 2004). Specimens have also been observed along the Pacific coast near Acapetagua and Huixtla, in southern Chiapas near the Guatemalan border (J. Campbell, pers. comm.). As do other Beaded Lizards, *H. h. alvarezi* appears generally to prefer tropical deciduous forest habitats.

H. h. alvarezi is distinguished from other Beaded Lizards primarily by its dark coloration. At birth *H. h. alvarezi* show a dorsal pattern and coloration similar to *H. h. horridum*, but as they mature the yellow spots and bars on the dorsum are gradually replaced by slate black, brown, or gray. Adults may be entirely black with faint traces of a light pattern, or with light yellow spots, especially posteriorly (plate 14). Yellow spots may remain on the tail, but adult *H. h. alvarezi* show none of the conspicuous tail banding evident in juveniles or in the other subspecies of *H. horridum* (plate 14). *H. h. alvarezi* has a broad, wedge-shaped mental scale that lacks the indentations of the shield-shaped mental scale possessed by *H. h. exasperatum* and some *H. h. horridum* (fig. 5d, e). In general, there do not appear to be any other obvious differences in scale characters between *H. h. alvarezi* and the other subspecies of *H. horridum*, except that some individuals of *H. h. charlesbogerti* have enlarged preanal scales (discussed below).

HELODERMA HORRIDUM CHARLESBOGERTI CAMPBELL AND VANNINI 1988
MOTAGUA VALLEY BEADED LIZARD OR ESCORPIÓN

Nearly 30 years after Bogert and Martín del Campo (1956) described *H. h. alvarezi*, a distinctive population of Beaded Lizards was described along Guatemala's Atlantic drainage. The type specimen was encountered by an agricultural laborer at Espíritu Santo (17 km E of El Rancho, Departmento de El Progreso, elevation 300 m) in southeastern Guatemala's Motagua Valley in September 1984 (Campbell and Vannini 1988). Twelve more specimens were later added, extending the known distribution of *H. horridum* by at least 230 km (Campbell and Vannini 1988). *H. h. charlesbogerti* was named after Charles M. Bogert, in honor of the foundation he and Rafael Martín del Campo provided on intraspecific variation in helodermatid lizards (see chap. 1).

Adult *H. h. charlesbogerti* differ from adult *H. h. alvarezi* in having a black dorsum distinctly marked with pale yellow spots, especially posterior to the insertion of the front limbs (Campbell and Vannini 1988). Juvenile *H. h. charlesbogerti* are similar to those of *H. h. alvarezi* and *H. h. horridum*, but the adults retain four to five pairs of distinctive light yellow tail rings each separated by a black band (plate 14; tail rings are absent in *H. h. alvarezi*). The background color of *H. h. charlesbogerti* is darker than that of *H. h. alvarezi* and *H. h. charlesbogerti* may have a relatively greater hind limb span than the other subspecies of *H. horridum* (Campbell and Vannini 1988). Some *H. h. charlesbogerti*, primarily females, appear to possess greatly enlarged preanal plates, a trait not found in other subspecies of *H. horridum* (Campbell and Vannini 1988; Ariano Sánchez 2003); however, subsequent analyses have shown this trait to be somewhat variable (J. A. Campbell, pers. comm.).

H. h. charlesbogerti is known only from the Río Motagua Valley and adjacent foothills of eastern and southeastern Guatemala (Campbell and Vannini 1988; Ariano Sánchez 2003). Its range appears to be separated from the nearest known populations of *H. h. alvarezi* in the Río Lagartero Depression (which drains into the Río Grijalva of Chiapas, Mexico) by some 230 km. It inhabits tropical dry forest habitats similar to those in other parts of the range of *H. horridum* in Chiapas and western Mexico (Campbell and Vannini 1988; Ariano Sánchez 2003), but annual rainfall in the Motagua Valley (<500 mm) is lower than most other tropical dry forests inhabited by *H. horridum* (see chap. 5). The distribution of *H. h. charlesbogerti* appears to be continuous between the Río Motagua Valley and the dry foothills of southeastern Guatemala (Campbell and Lamar 2004).

HELODERMA SUSPECTUM COPE 1869

The first official description of a Gila Monster was published in a report on reptiles of the international boundary between the United States and Mexico (Baird 1859). Baird provided an accurate drawing of a Gila Monster but identified the lizard as "*Heloderma horridum.*" Ten years later, after examining Baird's report and other specimens, E.D. Cope described the lizard as a new species, choosing the binomial *Heloderma suspectum* because it was "suspected" to be venomous (Cope 1869). The type specimen reported by Baird came from Sierra de Moreno near Monument no. 146, one of the markers on the International Boundary between Sonora, Mexico, and Pima County, Arizona, southwest of Tucson (Bogert and Martín del Campo 1956).

H. suspectum is a shorter, chunkier, less arboreal lizard than is *H. horridum*, with more striking patterns and coloration. Adults reach a snout-to-vent length of 300–360 mm, an overall length of 350–500 mm, and a mean adult body mass of about 500 g (see chap. 6). Wild individuals may rarely approach 550 mm in overall length and weigh up to 1 kg. Males become reproductive at a SVL of 221 mm; females at a SVL of 239 mm (Goldberg and Lowe 1997). Males have wider heads than do females (Gienger and Beck unpubl. ms.).

H. suspectum occurs in parts of the Mohave Desert in extreme southeastern Nevada, southwestern Utah, southeastern California, and northwestern Arizona; throughout much of the Sonoran Desert region in Arizona, Sonora, and extreme northern Sinaloa, Mexico; and into a small part of the Chihuahuan Desert region in southeastern Arizona and southwestern New Mexico (see fig. 6). It ranges in elevation from desert-scrub habitats near sea level up to about 1,738 m (5,700 ft) in pine/juniper or pine/oak woodland communities (see chap. 5). Gila Monsters have been observed within sight of the beach in Sonora, Mexico (B. E. Martin, pers. comm.). Specimens have been collected up to 1,708 m (5,600 ft) in the foothills of the Catalina Mountains north of Tucson, Arizona (University of Arizona collection records). In June 2003, R. Babb (pers. comm.) collected a DOR (dead on the road) specimen in pine/juniper woodland north of Globe, Arizona. This record increased the validated elevational range of *H. suspectum* to 1,738 m (5,702 ft). There are reported sightings of Gila Monsters in woodland and forest habitats above 1,830 m (6,000 ft) in the Arizona–Sonora borderland mountains but these reports remain unverified.

Throughout their range, hatchling and juvenile *H. suspectum* have a similar pattern consisting of four to five black saddlelike crossbands on a pale yellow or pale orange background and four to five black bands on the tail. Bogert and Martín del Campo (1956) noticed that adult specimens from populations of western Arizona, extreme southeastern Nevada, and southwestern Utah retained most of the pattern characteristics of the hatchling. They designated this group as a new subspecies, *H. s. cinctum*, or the Banded Gila Monster (plate 15). Adult specimens, which they examined throughout the remainder of the range in southern Arizona, southwestern New Mexico, and Sonora, Mexico, showed an irregular "reticulated" pattern of black mottles or blotches on a rose, orange, or yellow background (see plates 16–18). In these individuals, an ontogenetic change in the dorsal pattern occurred where the distinct bands found in juveniles seemed to break up into the reticulate pattern characteristic of adults. Bogert and Martín del Campo (1956) designated this subspecies the Reticulate Gila Monster, *H. s. suspectum*. These authors also noticed a trend in coloration in *H. suspectum* wherein individuals from northern populations (i.e., Nevada, Utah, northwestern Arizona) were lighter and those from the south (i.e., southern Arizona and Sonora) were darker in coloration.

The general pattern that Bogert and Martín del Campo (1956) identified for *H. suspectum* still holds partially true today. Individuals from Nevada seem to consistently show strong banding (plate 15), and most lizards from other northerly populations tend to be lighter in color than those farther south. However, there are notable exceptions. Dark adults, devoid of any remnant of the banded juvenile pattern, have been discovered in black basaltic lava flows in southwestern Utah (Beck 1985a; plate 15), a region near the northern periphery of the range where only lighter-colored, banded adults were previously thought to occur (Bogert and Martín del Campo 1956). In coloration and pattern, these Gila Monsters resemble individuals from Hermosillo, Sonora (in the southern portion of the range) more than they do *H. s. cinctum* from the north. Dark, Reticulate Gila Monsters have also been observed in California (Lovich and Beaman, unpublished manuscript; Bicket 1982). In addition, adult lizards from southwestern New Mexico (at our Redrock study site), in the heart of the range of *H. s. suspectum* described by Bogert and Martín del Campo (1956), commonly show the lighter, banded pattern characteristic of *H. s. cinctum* populations to the north (see plates 15 and 17).

These observations suggest that the banded and reticulate morphs of *H. suspectum* do not conform to the original geographic patterns described by Bogert and Martín del Campo (1956). Neither does evidence from mtDNA variation fully support the current designation of the banded and reticulate subspecies. Banded individuals from southwestern Utah, near the northern terminus of their geographic distribution, show little divergence in mtDNA base sequences from "reticulate" individuals in Hermosillo, Sonora, 1,100 km (650 miles) to the south (Douglas et al. 2003). In contrast, *H. h. exasperatum* shows a sequence divergence of 6.1% from its nearest subspecies *(H. h. horridum)* sampled 1,500 km (900 miles) away. *H. s. cinctum* from southern Nevada show 0.5% base sequence divergence from other *H. suspectum* populations (Douglas et al. 2003). This suggests designation of a northern subspecies of *H. suspectum* may still be warranted, but its distribution may be more restricted than previously thought and it may not be based solely on the dorsal pattern. Additional specimens are needed, especially from California, and additional microsatellite DNA markers should be examined before we have a complete understanding of genetic variation and subspecies relationships of *H. suspectum*. Pending a more thorough review of the genetic evidence, I'll recognize the same subspecies described by Bogert and Martín del Campo (1956). The reader should keep in mind that the banded/reticulate dichotomy in *H. suspectum* may be useful in describing variation in dorsal patterns but may not accurately portray geographic patterns that normally indicate distinct subspecies.

HELODERMA SUSPECTUM SUSPECTUM COPE 1869
RETICULATE GILA MONSTER

This subspecies has been distinguished from most populations of *H. s. cinctum* by an ontogenetic change in its dorsal pattern (Bogert and Martín del Campo 1956). Juveniles of the two subspecies are indistinguishable, but in *H. s. suspectum* the bandlike juvenile pattern usually breaks up to form an irregular, reticulated pattern of black mottles or blotches on a rose, orange, or yellow background. *H. s. cinctum*, on the other hand, retains most of the pattern characteristics of the hatchling throughout its life.

In Mexico, *H. s. suspectum* occurs in Sonoran desert-scrub habitats throughout much of Sonora, from coastal desert north of Kino Bay and thornscrub habitats near Alamos, into drainages of the Río Fuerte in southern Sonora and northern Sinaloa (see fig. 6). A single specimen known from El Dorado, Sinaloa, about 280 km south of the closest locality, suggests that the species may once have ranged into central Sinaloa (Bogert and Martín del Campo 1956; Campbell and Lamar 2004).

In Arizona, *H. s. suspectum* occurs in desertscrub, semidesert grassland, and (more rarely) woodland habitats in nine counties (Cochise, Gila, Greenlee, Graham, Maricopa, Pima, Pinal, Yavapai, and Yuma; see fig. 6). Gila Monsters are generally found wherever Arizona Upland desert-scrub habitats occur, but they also commonly frequent semidesert grassland (see chap. 5). *H. s. suspectum* is thought to intergrade with the reticulate subspecies *(H. s. cinctum)* from just northwest of Wickenburg along a line drawn southwest through the Mohawk mountains to the border with Sonora, Mexico.

The presence of the Gila Monster in New Mexico was not confirmed until the early 1950s (Shaw 1950; Koster 1951), even though they can be locally abundant in some areas. *H. s. suspectum* occurs in New Mexico along the Gila River Valley from the Arizona border eastward to the vicinity of Redrock (Grant Co.), and southward to the eastern slopes of the Peloncillo Mountains (Hidalgo Co.) near the border with Sonora, Mexico. Records are known from Hidalgo, Grant, Luna, and perhaps Dona Ana counties at elevations of 1,180–1,950 m (3,700–6,400 ft; Campbell 1976; Degenhardt et al. 1996). In addition, there are documented records northward to the vicinity of Cliff (Grant Co.) and eastward to near Las Cruces; however, these are suspected to be unnatural occurrences for this lizard (Degenhardt et al. 1996). Records from Kilbourne Hole in Dona Ana County and other areas east of a line from Silver City southward to Animas may represent displaced, released, or escaped captives (Degenhardt et al. 1996).

Bogert and Martín del Campo (1956) mentioned an individual captured 15 miles northwest of Lordsburg, New Mexico, that "still had many of the pattern characteristics of juvenile *H. s. suspectum*, although it was larger than most juveniles." This lizard measured 277 mm SVL, a size we now know is well beyond the minimum for sexual maturity (Goldberg and Lowe 1997). We also know now that many individuals from southwestern New Mexico (e.g., our Redrock study site; Beck and Jennings 2003) retain the banded pattern of juveniles (see plate 17), even though they occur within the range of what Bogert and Martín del Campo (1956) described as that of *H. s. suspectum.*

HELODERMA SUSPECTUM CINCTUM BOGERT AND MARTÍN DEL CAMPO 1956

BANDED GILA MONSTER

Adults of this subspecies tend to be lighter in color and retain the juvenile pattern of wide black crossbands on a normally yellowish pink background (plate 15). Exceptions include dark individuals (without crossbands) found in black basaltic lava flows in southwestern Utah (Beck 1985a) and in the Piute Mountains of southeastern California (Bicket 1982; see below) as well as light, banded adults from southwestern New Mexico (plate 17). The type locality of this subspecies is "Las Vegas, Clark County, Nevada, at an elevation of 2,033 (620 m) feet in the Las Vegas Valley" (Bogert and Martín del Campo, 1956).

Heloderma suspectum cinctum is found in western Arizona from as far north as the Arizona Strip (near Littlefield) to the Colorado River (Mohave Co.) to the southwestern edge of the Central Plateau in southwestern Yavapai County, to near Yuma in the south (Bogert and Martín del Campo 1956; Funk 1966). Specimens have been recorded from La Paz, Maricopa (especially near Wickenburg), Mohave, Yavapi, and Yuma counties (see fig. 6). *H. s. cinctum* normally occurs in rocky habitats along the foothills of desert mountains, occasionally venturing into sandier valleys where appropriate microhabitats can be found (chap. 5).

In California, the earliest recorded sighting of *H. suspectum* was a specimen from the "Mohave River" in San Bernardino County (Baird 1859). Subsequent researchers questioned this record, as well as other early observations of Gila Monsters in California (Woodson 1949; Bogert and Martín del Campo 1956; Tinkham 1971a). However, records of *H. s. cinctum* in California have now been verified from the Clark, Kingston, Piute, and Providence mountains of eastern San Bernardino County and part of the Kingston Range in Inyo County (Bradley and Deacon 1966; DeLisle 1979, 1983; Ford 1981; Bicket 1982; Lovich and Beaman, unpublished manuscript). De Lisle reported nine lizards from the Providence Mountains in 1982. An individual observed and photographed by Bicket (1982) in the Piute Mountains showed the darker coloration and mottled pattern representative of the reticulate morph, *H. s. suspectum* (Lovich and Beaman unpublished ms). Other California records of *Heloderma* include the Blythe Airport (Woodson 1949), 40.2 km northeast of Desert Center in the Chuckwalla Mountains (Tinkham 1971a; both in Riverside Co.), and the Imperial Dam on the Colorado River in Imperial County (Funk 1966), although no specimens or photographs are available to verify these observations. The known elevational range of *H. s. cinctum* in California extends from 45 m along the lower Colorado River to at least 1,100 m in the Clark Mountains.

H. s. cinctum occurs in southeastern Nevada in Clark and Lincoln counties from near Laughlin in the south to near Caliente in the north (Gienger 2003; see fig. 6). As is true throughout the Mohave Desert, Gila Monsters show a patchy distribution in Nevada, inhabiting some of the rocky canyons, washes, and sandy valleys that drain desert mountain ranges in this region. Adults from Nevada appear to consistently retain the dorsal crossbands present in juveniles (plate 15).

In Utah, the Gila Monster also shows a patchy distribution, occurring among rocky slopes, washes, and sandy valleys at the base of sandstone bluffs. *Heloderma suspectum cinctum* is found in Utah only within Washington County, from the Red Cliffs recreation area around Leeds, southwest to the Beaver Dam slope on the Arizona border (Beck 1985b; Fridell et al. 1998). Once locally abundant around the communities of Bloomington, St. George, Santa Clara, and Washington, Gila Monsters have been extirpated from much of their former habitats by the development boom occurring in southwestern Utah (chap. 9).

WHAT LIMITS THE DISTRIBUTION OF *HELODERMA*?

Doubtless, the current distribution of helodermatid lizards results from a combination of biotic factors (e.g., predation and competition) and abiotic ones (e.g., temperature and moisture). A conservative energy-use strategy that permits helodermatid lizards to subsist for long periods without food serves them well in environments where resource availability fluctuates, such as tropical dry forests and deserts. Helodermatid lizards may thus have a competitive advantage in highly seasonal environments, while becoming more vulnerable to competition and predation in wetter, more stable tropical environments that would require greater foraging activity throughout more of the year (chaps. 4 and 5). In less seasonal habitats Beaded Lizards might be more exposed to potential predators and competitors. Perhaps that is the reason why *H. horridum* does not penetrate deeper into the wet tropics. Farther north, colder winters and a compressed warm season may restrict opportunities for foraging on nests. Moreover, warm nights may be important for foraging during summer, especially for juvenile *H. suspectum* (chap. 5).

Helodermatid lizards are found in habitats where a significant portion of annual precipitation falls during summer (Bogert and Martín del Campo 1956). *Heloderma suspectum* is conspicuously absent from regions of the North American deserts (i.e., much of the Mohave and Lower Colorado deserts), where summer rainfall is below 25% of the total annual precipitation (chap. 5). Very dry summers present a problem for a widely foraging nest predator with leaky skin (see chaps. 4 and 5). It is probably juveniles, who forage on warm summer nights for lizard eggs, who would be most severely influenced by consistent summer drought. Summer rain may also provide critical opportunities for rehydration.

Part of an explanation for what limits the distribution of helodermatid lizards (although admittedly quite speculative at this point in our understanding) might relate to their nesting biology (see chap. 8). Eggs are stuck in a nest and cannot escape unfavorable extremes in temperature and soil moisture. Eggs may, therefore, be at least as sensitive as adult lizards are to climatic factors. *Heloderma suspectum* lay eggs just as the summer rains begin (chap. 8) and that rain may be vital for setting up proper moisture conditions within the nest environment. Eggs of helodermatid lizards are extremely sensitive to moisture conditions during incubation (North 1996; Seward 2000). More consistently dry summer soil conditions could keep Gila Monsters out of the western Mohave Desert.

In contrast to Gila Monsters, *H. horridum* eggs are laid in late fall near the end of the rainy season (chap. 8). The relatively warmer soil temperatures of tropical dry forest habitats during winter might be necessary for incubation and thus restrict the distribution of *H. horridum* to tropical habitats. And perhaps a prolonged winter dry season—such as occurs throughout the range of *H. horridum*—may be necessary for eggs to avoid decomposing from too much soil moisture, which can be a problem for eggs incubated in captivity (Applegate 1991; North 1996).

The nesting biology of helodermatid lizards is still poorly understood. Actual nest conditions and incubation periods in nature are still unknown (chap. 8). Future research on their nesting biology might help test the admittedly speculative hypothesis that incubation conditions influence the distribution of helodermatid lizards. On the other hand, many believe that the distribution of contemporary helodermatid lizards is influenced by the legacy of their tropical origins (Lowe et al. 1986; Pregill et al. 1986). A look at their fossil ancestors, who showed a much broader geographic distribution, might give us further insight.

THE FOSSIL RECORD

The earliest fossil of a helodermatid lizard comes from Cretaceous (Albian-Cenomanian) mudstones of central Utah and is nearly 100 million years old (Cifelli and Nydam 1995; Cifelli et al. 1997; Nydam 2000). This fossilized creature, designated *Primaderma nessovi*, represents the oldest known member of the Monstersauria, a distinct clade of lizards that includes *Heloderma* and its fossil relatives (Norell and Gao 1997). The Monstersauria roughly corresponds to the Helodermatidae (Norell and Gao 1997; Gao and Norell 1998, 2000; Balsai 2001) and for this discussion can be regarded as synonymous. A venomous relative of *Primaderma*, *Estesia mongoliensis*, was uncovered in 1992 from a Late Cretaceous sandstone cliff in south-central Mongolia (Norell et al. 1992; Norell and Gao 1997). The discovery of these two fossils extended the known age of the helodermatid clade well into the Cretaceous, before many species of dinosaurs had even appeared. These fossil discoveries also leave open the possibilities of either a North American or an Asian origin of helodermatid-like platynotans. In addition to *Primaderma* and *Estesia*, five additional genera, including *Heloderma*, appear as fossils between the Late Cretaceous and the Miocene. These fossil ancestors of *Heloderma*, and the likely environments they inhabited, are discussed below.

THE CRETACEOUS FOSSILS, 100–65 MILLION YEARS AGO

PRIMADERMA NESSOVI NYDAM 2000

Primaderma nessovi was discovered in a mudstone unit (the Mussentuchit Member) at the top of the Cedar Mountain Formation, Emery County, Utah (Cifelli and Nydam 1995; Nydam 2000). The most constrained date for these mudstones, based on ^{40}Ar/^{39}Ar determinations (Cifelli et al. 1997) is 98.39 ± 0.07 mya (million years ago). *Primaderma* is recognizable as a helodermatid-like platynotan in the diagnostic shape and structure of its teeth (but without obvious venom grooves), reduced tooth count, and fused, fragmented osteoderms on its skull. These traits are derived characteristics of platynotans that now appear to have evolved much earlier than previously thought. They clearly show that monstersaurs had a presence in North America nearly 100 million years ago.

Based on the structure of its skull, jaws, and teeth, *Primaderma* is believed to have been slightly larger than living *H. suspectum* and highly predaceous. It lived in a more mesic environment than do most contemporary helodermatids. With a rounded snout and bladelike, serrated teeth, *Primaderma* presumably foraged on relatively large vertebrate prey, having a niche similar to that fulfilled by many contemporary varanid lizards (see below). Even in light of its lack of venom grooves, phylogenetic analysis places *P. nessovi* firmly within the Monstersauria and adds support to previous suggestions (e.g., Pregill et al. 1986) that helodermatid lizards have undergone relatively little morphological change in their long history (Nydam 2000).

PALAEOSANIWA CANADENSIS GILMORE 1928

This ancient taxon (*Palaeo*, meaning "ancient," and *saniwa*, meaning "rock lizard"), previously thought to have been a varanid, has been reexamined and placed in the Monstersauria (Balsai 2001). Balsai examined earlier fragments of vertebrae from Canada and Montana, as well as new material consisting of two skulls, lower jaws, teeth, vertebrae, ribs, and parts of front and hind limbs, from at least two individuals from Montana. Phylogenetic analyses of these skeletal elements place these fossils squarely within the Monstersauria (Balsai 2001). *Palaeosaniwa* was a medium-sized predator, approximately 1½ to 2 m long with osteoderms on its head and possibly its neck. It had finely serrated teeth with trenchant margins thought to be precursors of the venom groove, a trait suggesting it may have been venomous.

Palaeosaniwa has been found in deposits ranging in age from the Late Campanian of Alberta, Canada (~83 mya), to the Late Maastrichtian Hell Creek Formation of Montana (~72.5 mya). Thus the genus endured for at least 10.5 million years, making it among the most persistent of monstersaurian taxa. *Palaeosaniwa* is believed to have inhabited both mesic and seasonally dry environments from what is now Alberta, Canada, to central and eastern Montana (Balsai 2001).

The extremely rich fossil beds of the Mongolian Gobi Desert (described by Gao and Norell 2000) have yielded numerous well-preserved fossils, including those of *Heloderma* and other Cretaceous ancestors, such as *Estesia* and *Gobiderma*.

ESTESIA MONGOLIENSIS, NORELL ET AL. 1992

This spectacular fossil, represented by a well-preserved skull, mandibles, and part of a front leg, was unearthed during the 1990 joint Mongolian–American paleontological expedition to the Gobi Desert of Mongolia. A subsequent visit to the same site in 1993 yielded a partial skeleton and associated braincase (Norell and Gao 1997). Also recovered at the site were associations of dinosaur eggs and a *Protoceratops* skeleton (Norell et al. 1992). The fossil beds are part of the Barun Goyot Formation and are considered Late Cretaceous/Middle Campanian in age (Norell et al. 1992), approximately 77 million years ago (although determination of its actual age is tenuous). *Estesia* was about 8 ft long and had teeth bearing deep longitudinal grooves very similar to extant *Heloderma*. Like many of its ancient and modern relatives, *Estesia* preyed upon vertebrates, perhaps even the nests of dinosaurs, which have been found in association with *Estesia* fossils (plate 6). Examination of the skeletal features of *Estesia*, and other platynotan fossils known at the time, prompted Norell and Gao (1997) to describe the Monstersauria clade, which contains extant *Heloderma* and its fossil relatives, including *Estesia*. *Estesia* was named in honor of Richard Estes (1932–1990), a vertebrate paleontologist who contributed greatly to our understanding of fossil lizards (Norell et al. 1992).

GOBIDERMA PULCHRUM BORSUK-BIALYNICKA 1984

Gobiderma, like *Estesia*, was discovered in Cretaceous deposits of the Gobi Desert of Mongolia (Borsuk-Bialynicka 1984; Gao and Norell 2000). The species name *pulchra* (Latin for "beautiful") was chosen "because of a beautiful state of preservation" of the holotype (Borsuk-Bialynicka, 1984; fig. 7b). *Gobiderma* is represented by at least four specimens from two separate geologic formations: the Djadokhta and Barun Goyot, which are believed to be Middle-to-Late Campanian in age (Gao and Norell 2000). The Campanian age occurred between 71 and 83 mya during the Late Cretaceous period. Some specimens of *Gobiderma* were unearthed from the same fossil beds as *Estesia*, suggesting that these two monstersaurian lizards were contemporaries. Like *Estesia*, *Gobiderma* was highly predaceous, but its teeth lacked venom grooves. It had conspicuous osteoderms, similar to those of modern *Heloderma* (fig. 7). When first discovered, *Gobiderma* was classified as a "Necrosaurian grade" within the Platynota (Borsuk-Bialynicka 1984) and was left unassigned by Pregill et al. (1986). Discovery of new specimens and more recent phylogenetic analyses, however, have shown that *Gobiderma* is the basal taxon of the Monstersauria (Norell and Gao 1997; Gao and Norell 1998, 2000; Nydam 2000).

The Cretaceous Gobi Desert ecosystem, where *Estesia* and *Gobiderma* lived, was believed to have been a semiarid desert with seasonal ponds and streams and some plant cover, similar to parts of today's Kalahari of East Africa (Gao and Norell 2000). Some of the Monstersaurian fossils were found in semihardened sand beds. Their absence of sand abrasion suggests quick burial and fossilization in a relatively moist environment within stable sand. Well-sorted, cross-bedded sandstones suggest the presence of large dune fields, but fluvial sediments suggest ephemeral water in the interdune environments. Runoff flowing from sand dunes during heavy rains probably covered dead or dying animals and buried others in their burrows. The presence of caliche paleosols suggests an arid desert when these rocks were deposited (Gao and Norell 2000).

PARADERMA BOGERTI ESTES 1964

This was the first Cretaceous fossil of a helodermatid to be discovered. A left maxilla and portions of other jaws and teeth were unearthed from the Lance Formation, a succession of continental sandstones and siltstone outcroppings in the Powder River Basin of eastern Wyoming, believed to be between 65 and 70 million years old (Estes 1964). Also found within the Lance Formation are fossils of some of the last dinosaurs to walk the earth, including *Tyrannosaurus rex* and *Triceratops horridus* (Spencer 2001). *Paraderma* showed a number of characteristics similar to *Heloderma*, including a reduced number of relatively heavy teeth (no more than nine in the upper jaw), osteoderms, and curvature of the nasal process of the maxilla, suggesting its snout was broad and depressed. Its stout jaws and sturdy skull architecture suggest it was well-equipped for subduing relatively large food items (Pregill et al. 1986). Based on the accompanying plant and animal fossils, and the sandstone/siltstone nature of the Lance Formation, *Paraderma* is thought to have inhabited a moist, subtropical environment similar to that of the coastal plains of the southeastern United States today (Estes 1964). *Paraderma* was placed in the Helodermatidae by Pregill et al. (1986) because of its helodermatid-like jaws and dental morphology. Because the teeth in fossil specimens of *Paraderma bogerti* were mostly broken, it is uncertain whether they conducted venom (Nydam 2000). *Paraderma* is also known from the Scollard Formation, central Alberta, and the Frenchman Formation, southwestern Saskatchewan, both Lancian/ Maastrichtian in age (Gao 1992).

THE TERTIARY FOSSILS, 40–5 MILLION YEARS AGO

EURHELODERMA GALLICUM HOFFSTETTER 1957

This fossil was exhumed from the Phosphorites of Quercy of France from Eocene–Oligocene deposits (Hoffstetter 1954, 1957; De Bonis et al. 1973), laid down approximately 38 million years ago. Additional material was discovered in Oligocene deposits at the phosphorite locality at Escamps, France (De Bonis et al. 1973). This species is represented by four almost complete maxilla, a lower jaw, pterygoids, parietals, and some vertebrae. It is distinguished from other helodermatids by its markedly constricted parietal (Pregill et al. 1986). *Eurheloderma gallicum* was larger than *H. suspectum*, but very similar morphologically. Its osteoderms were larger and fewer in number than those of extant *Heloderma*, and its teeth had a shallower venom groove, suggesting a less specialized venom apparatus (Bogert and Martín del Campo 1956).

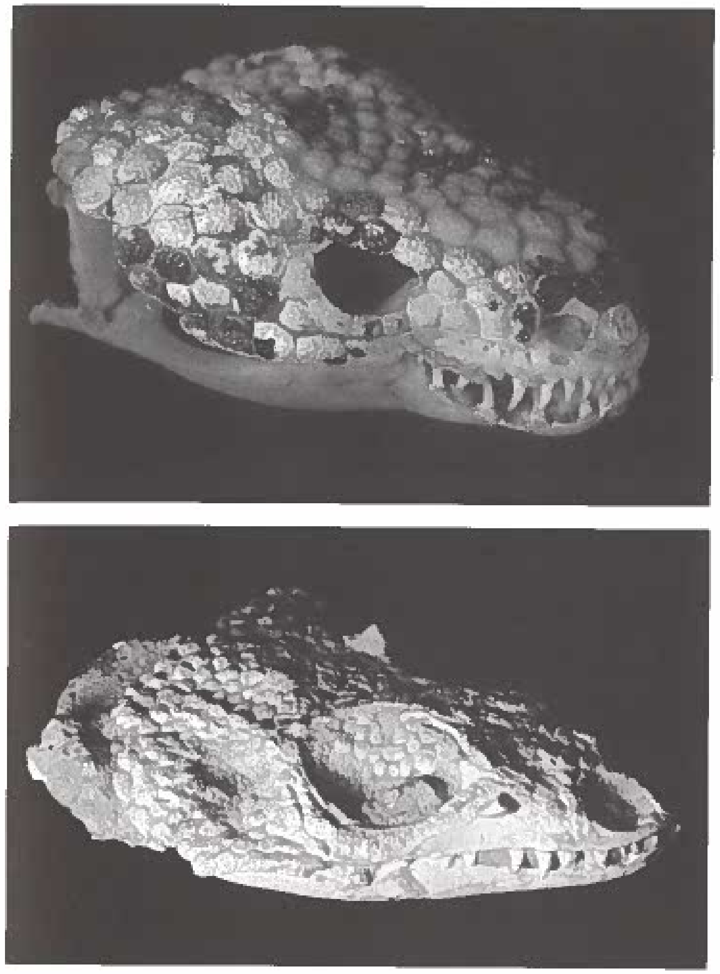


FIGURE 7. Skull of *Heloderma suspectum* (top) compared with a 70-plus-million-year-old fossil relative, *Gobiderma pulchra* (bottom), named because of its "beautiful state of preservation" (*pulchra* is Latin for "beautiful").

The Late Eocene–Early Oligocene environment of France is thought to have been warm, humid, and subtropical, perhaps turning slightly more open and dry toward the end of the Eocene (Gruascavagnetto and Kohler 1992; Kvacek and Erdei 2001).

CONFEREE *EURHELODERMA* BARTELS 1983

This fossil is represented by an isolated parietal from Paleocene–Eocene Bighorn Basin deposits of Wyoming (53–55 mya; Bartels 1983). Originally described as an unspecified varanoid, subsequent examination by Pregill et al. (1986) showed this fossilized parietal closely resembled that of *Eurheloderma*, suggesting that this European genus may have also occurred much earlier in North America. The taxon was left unassigned pending discovery of additional material (Pregill et al. 1986). The environment in which this fossil originated is thought to have been subtropical with a variety of aquatic habitats and lots of dry ground between streams and ponds. Temperatures were equable with no hard freezes (Bartels 1983).

LOWESAURUS MATHEWI GILMORE 1928

Lowesaurus mathewi represents a reassignment of *H. mathewi* (Gilmore 1928) to this new taxon based on its diagnostic triangular frontal bones (Pregill et al. 1986). *Lowesaurus* was named in honor of Charles H. Lowe in recognition of his many contributions to our knowledge of North American ecology (see chap. 1). It is represented by fossil material from the Oligocene of Colorado and Oligocene/Miocene of Nebraska. A partial maxilla showing unique grooved teeth (Gilmore 1928) and a complete right maxilla (Yatkola 1976) were found in the White River Formation, middle Oligocene (Orellan, ~34 mya) of Logan County, Colorado. The Nebraska specimens come from two different deposits in Morrill County. They include a partial skull (Yatkola 1976) from the Brule Member, White River Formation (Late Oligocene, Whitneyan, ~32 mya) near Redington, and a nearly complete right frontal bone and two trunk vertebrae from the Mitchell Pass Member, Gering Formation (Early Miocene, Arikareean, ~23 mya) near Bridgeport (Pregill et al. 1986). *Lowesaurus* possessed the distinctive teeth of a helodermatid, both in number (a reduced tooth count is a helodermatid characteristic; *Lowesaurus* had 11 maxillary teeth, *Heloderma* has 6–9) and in showing a distinctive venom groove, although not as pronounced as in *Heloderma* (Yatkola 1976; Pregill et al. 1986). *Lowesaurus* was believed to be somewhat smaller than living *Heloderma*. However, a precise estimate of the adult size of most of the tertiary fossil specimens is difficult to gauge because many of the reliable signs of adulthood (e.g., fusion of the epiphyses, basiocranial elements, girdles) have not been preserved (Pregill et al. 1986). The Late Oligocene and Early Miocene ecosystems of northeastern Colorado and southwestern Nebraska, where *Lowesaurus* fossils have been found, are thought to have been warm temperate forests and savannas of mixed trees and grasslands (National Park Service 1980). These habitats were warm temperate, but not tropical.

HELODERMA TEXANA STEVENS 1977

A complete skull of the closest fossil relative of modern *Heloderma* was discovered in early Miocene deposits of the Delaho Formation (later Arikareean age, ~23 mya) near Big Bend National Park, west Texas (Stevens 1977). *H. texana* had teeth with well-developed venom grooves and slightly less flattened osteoderms than do living *Heloderma* (Stevens 1977). It was thought to have been smaller and, based on its convex basioccipital, slightly more "varanid-like" than living species of *Heloderma*. The holotype of *H. texana* described by Stevens (1977) may actually be a subadult (Pregill et al. 1986), so its adult size may not be precisely known. Stevens (1977) suggested that the Early Miocene of Texas was a more humid environment than that inhabited by most *Heloderma* today and that contemporary *Heloderma* have withdrawn to drier tropical or subtropical habitats. The Early Tertiary plant fossil record from the western United States includes a large number of tropical dry forest elements (Graham and Dilcher 1995). These include the late Mid-Eocene Green River flora of Utah and Colorado (MacGinitie 1969) and California (Raven and Axelrod 1978).

Several other fossil discoveries of possible *Heloderma* ancestors have been left unassigned until additional material is discovered (or until someone finds the time to scrutinize their characteristics) that will allow more complete analyses of phylogenetic relationships. For example, Estes (1983) illustrated a vertebra from the Early Miocene of Florida that he described as *Heloderma*-like. Gao (1992) mentions *Labrodioctes montanensis*, a large (1.5 m SVL) helodermatid from the Judith River Formation of Montana and the Oldman Formation of Alberta, Canada, both Judithian/Campanian in age (~72–75 mya).

RECENT FOSSILS

The fossil record of the Helodermatidae is summarized in table 3. There is a large gap in the fossil record between the time of *H. texana*, approximately 23 million years ago, and more recent *H. suspectum* fossils, the oldest of which is approximately 22,500 years old (Van Devender 1990). Fragments of skin, osteoderms, and vertebrae of *H. suspectum* have been found in cave deposits (Brattstrom 1954; Mead and Phillips 1981; Mead et al. 1984) and ancient packrat middens (Van Devender 1990) ranging in age from approximately 2,000 to 23,000 years old in southern Nevada and Arizona (see table 3). None of these Quaternary fossils occurs outside of the region currently occupied by *H. suspectum*. They suggest that the Gila Monster was well established in the American Southwest during the Late Pleistocene and the Holocene of the past 25,000 years in desert, grassland, and woodland habitats (Mead and Philips 1981; Mead et al. 1984; Van Devender 1990).

PHYLOGENY

Helodermatid lizards have traditionally been placed in the Platynota, a taxon used by Camp (1923) to include Varanoidea (represented today by *Varanus*, *Lanthanotus*, and *Heloderma*) and Mosasauroidea (represented only by fossils). McDowell and Bogert (1954) used Platynota as an alternate name for Varanoidea, as have others (Rieppel 1980, 1988; Borsuk-Bialynicka 1984). Pregill et al. (1986) recommended Platynota be used only as a "term of convenience" because the monophyly of the group had not been established at that time. However, more comprehensive analyses (Lee 1997; Gao and Norell 1998, 2000) have established monophyly of the Platynota and redefined the group as "the most recent common ancestor of Monstersauria and Varanidae, and all its descendents" (Gao and Norell 1998), a definition similar to Camp's (1923) original usage. Based on the structure of their jaws and teeth, predatory habits are believed to be a basal platynotan characteristic. Figure 8 shows a cladogram for the Helodermatidae (i.e., Monstersauria) based on analyses by Nydam (2000), Gao and Norell (2000), and Norell and Gao (1997).

RELATIONSHIPS WITH *VARANUS*

As a member of the Platynota, *Heloderma* shares a more recent common ancestor with the Varanidae than with any other extant lizard group (Estes et al. 1988). Helodermatids are the New World equivalent of a sluggish, venomous monitor lizard. The demeanor, gait, and general body form of the Mexican Beaded Lizard are sufficiently reminiscent of *Varanus* that many familiar with *H. horridum* call it the "Mexican monitor." The helodermatids are similar to *Varanus* in many other respects, such as several skeletal features, osteoderms (a diagnostic trait of *Heloderma* and also present in many species of *Varanus*), their specialized chemosensory systems, and their spectacular ritualized male combat behavior (McDowell and Bogert 1954; Rieppel 1980; Pregill et al. 1986; Estes et al. 1988; Beck and Ramírez-Bautista 1991). The precursor of *Heloderma*'s venom apparatus, the Gland of Gabe, is also possessed by varanid lizards (Kochva 1974; Gabe and Saint Girons 1976; Pregill et al. 1986). Similarities between varanid and helodermatid lizards in the structure of the nasal capsule add support to earlier conclusions about their close evolutionary affinities (Bernstein 1999).

Helodermatids also have a number of skeletal characteristics that set them apart from the varanids, including a steep nasal process of the maxilla, which gives them a more rounded muzzle and shorter face than *Varanus* (Estes et al. 1988). Helodermatid lizards have tails used for fat storage that are shorter than tails of most varanid species, as well as a shorter, fatter tongue that includes a villous basal portion and no sheath (Bogert and Martín del Campo 1956; Schwenk 1988). Helodermatid lizards do not tolerate the high body temperatures sustained by varanid lizards. Their preferred temperature

TABLE 3

Fossils of Helodermatid Lizards

	AGE	LOCATION	REFERENCES	HABITAT
1 *Heloderma suspectum* (skin fragments/osteoderms)	8,000–10,000 years ago	Gypsum Cave, Near Las Vegas	Brattstrom 1954	
Heloderma suspectum sacral vertebrae	<13,000 years ago	Vulture Cave, Grand Canyon, Arizona	Mead and Phillis 1981	Juniper woodland?
Heloderma suspectum (osteoderms)	22,000–22,760 years ago	Waterman Mountains, Arizona	Van Devender 1990	Juniper, Pinyon, Joshua tree, Arizona rosewood
Heloderma suspectum (vertebra)	8,000–12,000 years ago	Deadman Cave, southern Arizona	Mead et al. 1984	Desert grassland/woodland
2 *Heloderma texana* Stevens 1977	Early Miocene (later Arikareean; ~ 23 mya)	Big Bend, Texas	Stevens 1977	Castolan local fauna
3 *Lowesaurus mathewi* Gilmore	Middle Oligocene (Orellan, 30–32 mya)	Logan Co., Colorado	Gilmore 1928	Cedar Creek Member, White River Formation
	Middle Oligocene	Logan Co., Colorado	Yatkola 1976	White River Formation
	Late Oligocene (Whitneyan)	Morril Co., Nebraska	Yatkola 1976	Brule Member, White River Formation
	Early Miocene (25–27 mya)	Morril Co., Nebraska	Pregill et al. 1986	Mitchell Pass Member, Gering Formation, Arikaree Group
4 *Eurheloderma gallicum* Hoffstetter 1957	Early Oligocene (~38 mya)	Phosphorites du Quercy, France	Hoffstetter 1957	
Eurheloderma gallicum Hoffstetter 1957	Oligocene	Phosphorites du Quercy, France	De Bonis et al. 1973	
5 Parietal similar to *Eurheloderma*, but specimen left unassigned	Latest Paleocene (54 mya?)	Bighorn Basin, Wyoming	Bartels 1983; Pregill et al. 1986	
6 *Paraderma bogerti* Estes 1963	Late Cretaceous (65–70 mya)	Wyoming	Estes 1964	Lance Formation
7 *Gobiderma pulchrum* Borsuk-Bialynicka 1984	Upper Cretaceous	Mongolia	Borsuk-Bialynicka 1984; Gao and Norell 2000	
8 *Estesia mongoliensis* Norell et al. 1992	Late Cretaceous (mid-Campanian, ~77 mya)	Mongolia	Norell et al. 1992; Norell and Gao 1997	Barun Goyot Formation
9 *Palaeosaniwa canadensis*	Campanian (73–84 mya)	Alberta, Canada; Teton Co., Montana	Balsai 2001	Various from wet to seasonally dry
10 *Primaderma nessovi* Nydam 1990	Middle Cretaceous (Albian-Cenomanian, 98 mya)	Utah	Cifelli and Nydam 1995; Nydam 2000	Mussentuchit Local Fauna, Cedar Mtn. Formation

NOTE: See text for more detailed descriptions of fossils and possible habitats.

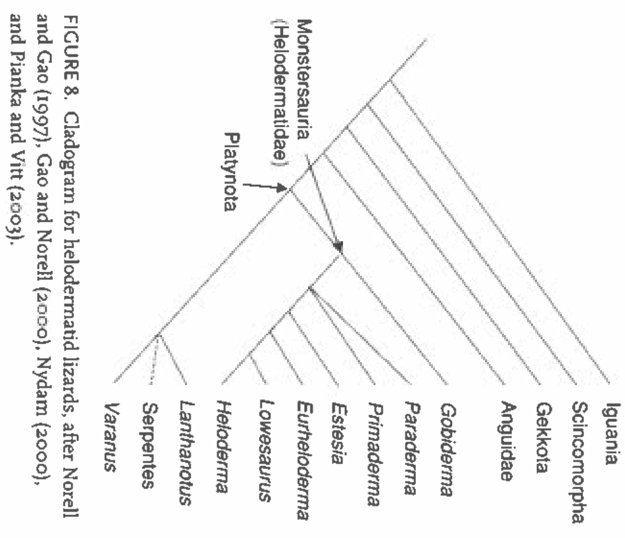


FIGURE 8. Cladogram for helodermatid lizards, after Norell and Gao (1997), Gao and Norell (2000), Nydam (2000), and Pianka and Vitt (2003).

during activity and basking is around 30°C (see chap. 4 on thermal biology). They begin seeking refuge at temperatures approaching 38°C and become paralyzed at 42°C, which is near their critical thermal maximum. Interestingly, helodermatids, like *Varanus*, also possess a high capacity to sustain aerobic activity, a trait they possibly inherited from their varanoid stock (John-Alder et al. 1983; Beck et al. 1995). A high aerobic capacity may seem surprising for such a sedentary lizard (contemporary *Heloderma* do not seem to need this capacity for normal foraging activity), but it may be advantageous during the intensive and physically exhausting combat rituals of male *Heloderma*. Males with superior strength and endurance more frequently emerge as winners during combat encounters and may thereby enjoy greater reproductive success. Male *Heloderma* have also been shown to have higher aerobic capacities than do females (Beck et al. 1995), which suggests that sexual selection may have played a role in shaping the high aerobic capacities of varanoid lizards.

The Varanidae showed much greater rates of speciation than did the Helodermatidae and radiated into a larger variety of regions and habitats. Today there are over 50 species of varanid lizards occupying habitats ranging from deserts to dense forests as well as mangrove swamps and savannas in Africa, Asia, and Australia (Pianka and King 2003). The helodermatids appear in comparison to be relicts of a bygone time.

RELATIONSHIPS WITH SNAKES

With the exception of their sister anguimorph taxa (e.g., lizard families Varanidae and Anguidae), the helodermatid lizards are more closely related to the snakes than they are to other extant lizards. Platynotan lizards, including *Heloderma*, share a number of characteristics in common with snakes. Both groups show similarities in their teeth and tooth replacement, the structure of their skulls and forked tongues, and behavioral traits such as their "male combat dance" (Estes et al. 1988; Beck and Ramírez-Bautista 1991; Lee 1997). The snakelike features of the Varanoidea have not escaped the attention of herpetologists, and a phylogenetic connection between snakes and platynotan lizards has long been suspected (e.g., Cope 1869; Camp 1923; McDowell and Bogert 1954). More recently, analyses (which included mosasauroid fossils) have validated the suspicions of earlier researchers of the phylogenetic relationship between snakes and platynotan lizards (Lee 1997; Gao and Norell 1998, 2000; Caldwell 1999; but see Rieppel and Zaher 2000). Helodermatid lizards also superficially resemble snakes in their foraging behaviors, their ability to take large meals, and especially in their spectacular combat rituals, which include many of the grappling postures exhibited by fighting male snakes (Shaw 1948a; Gillingham 1987; Beck 1990; Beck and Ramírez-Bautista 1991). The platynotan lizards might even be more appropriately regarded as "legged snakes" than as lizards! The venom system of *Heloderma*, however, is quite different from that of snakes and appears to have evolved independently (see chap. 3).

INTERPRETATIONS OF THE FOSSIL RECORD AND EVOLUTIONARY SCENARIOS

By examining skull fragments and other material found in association with helodermatid fossils, what can be pieced together about the ecology and evolution of these ancient lizards? The Helodermatidae (i.e., Monstersaurian clade) is indeed an ancient and persistent lineage. Its fossil record extends back at least 98 million years. Family members somehow managed to survive the great Cretaceous extinctions, which vanquished the dinosaurs 65 million years ago. The two remaining species of helodermatid lizards are relicts of a more diverse lineage that included at least six other genera distributed in Asia, Europe, and North America. Additional fossil relatives of *Heloderma* likely still await discovery, and, because fossilization is a relatively rare and sporadic phenomenon, others undoubtedly left little trace of their existence and will never be known. The majority of fossils recognizable as helodermatid consist primarily of skulls and jaw material (see table 3), which may reveal important information about feeding ecology and adaptations, but show us only a fragment of the whole evolutionary puzzle. The material lacking from the fossil record, such as girdles, limbs, soft tissues, and the ecological traits they might reveal, remain unknown. Moreover, the fossil material available from which we can reconstruct an evolutionary scenario for *Heloderma* is very old. No fossils of *Heloderma* have been found between the Early Miocene (~23 mya) and the Late Quaternary (~23 thousand years ago). What evolutionary developments happened during the intervening years is largely a matter of conjecture. Nevertheless, careful skeletal analyses reveal that modern *Heloderma* appears little changed from its ancient relative, *H. texana*, and helodermatid lizards in general have undergone relatively little gross morphological change over their long evolutionary history. They are thus regarded by many as living fossils (Pregill et al. 1986; Nydam 2000).

The ancient Monstersaurians occurred in a broader range of environments than those inhabited by *Heloderma* today. They included forests, deserts, edges of swamplands, and perhaps even savannas. With the exception of the Cretaceous habitats of southern Mongolia, which were probably dune-filled semiarid deserts with seasonal ponds and streams, most of the ancestral environments appeared wetter than the desert, semidesert, and subtropical habitats that harbor Gila Monsters and Beaded Lizards today. The more recent helodermatid fossils (i.e., *L. mathewi* and *H. texana;* table 3) lived in warm, seasonal temperate forests that were probably wetter than most habitats inhabited by *Heloderma* today (Stevens 1977; Pregill et al. 1986). If *Heloderma* had its origins in moist environments, as the fossil record suggests, such a history may explain why Gila Monsters and Beaded Lizards have leaky skins, a trait that might seem puzzling given the dry environments they inhabit today (DeNardo 2004; chap. 4).

EVOLUTION OF A SEDENTARY LIFESTYLE

Fossil evidence also suggests that the ancestral helodermatids were all highly predaceous. Their stout jaws and sturdy skull architecture enabled them to consume relatively large prey items (Pregill et al. 1986; Nydam 2000), some of which likely included the contents of vertebrate nests, perhaps even dinosaur eggs and hatchlings (Norell et al. 1992; plate 6). Some of the *Heloderma* ancestors, such as *Estesia* and *Gobiderma*, are believed to have filled an ecological role similar to that of contemporary varanid lizards. One of the traits that is believed to have set the helodermatids on a track separate from the varanids is their ability to take relatively large prey items (Pregill et al. 1986). Varanid lizards diverged early toward a feeding mode directed at more mobile prey, using their serrated teeth to tear flesh before swallowing smaller morsels. This strategy required a more active lifestyle and the ability to chase down and subdue moving prey. Ancestral varanids are thus believed to have been larger, more active predators than helodermatids, feeding more commonly on adult vertebrates that were probably small relative to their own body size (Pregill et al. 1986). Ecological and physiological features of modern varanid lizards support such a lifestyle. They are generally quite active and have relatively high metabolic rates and, for lizards, an exceptional ability for endurance and sustained aerobic activity (Bennett 1983). Most modern varanid lizards also feed on relatively small prey items. Predation on large vertebrates (e.g., by *Varanus komodoensis;* Auffenberg 1981b) is believed to be a derived condition within the Varanidae and involves ingestion of pieces, rather than large, intact items (Pregill et al. 1986). Where and when this divergence took place is still open to debate because ancient helodermatid fossils occur in Asia and North America (as well as France). The varanid lizards are believed to have originated in Asia (Estes 1983; Fuller et al. 1998).

Helodermatid lizards, on the other hand, diverged toward a more inactive lifestyle characterized by long periods spent without foraging or feeding. During the Miocene, when the North American climate became drier and more variable, it is thought that *Heloderma* became more specialized toward drier subtropical and desert environments (Stevens 1977; Pregill et al. 1986). The low-energy strategy shown by contemporary helodermatid lizards is adaptive for life in the dry, harsh, seasonal environments that they came to exploit during and after the Miocene.

EVOLUTION OF VENOM

In contemporary helodermatid lizards, the venom system clearly plays a primary role in defense (see chap. 3). Several of *Heloderma*'s ancestors (i.e., *Lowesaurus, Eurheloderma*, and *H. texana*) also had teeth with venom grooves. Were these venomous weapons also used for defense, or were they used to acquire food, or for both purposes? We may never know for certain. The evolution of the massive skull and stout jaws in helodermatid ancestors may have been adaptations for feeding on larger prey; teeth-bearing venom grooves may have aided in subduing such struggling prey (Pregill et al. 1986). In this scenario, a venom system could easily have served a role in prey acquisition, especially if ancestral diets included prey better equipped to resist being swallowed than the defenseless nestlings and eggs included in helodermatid diets today.

An ability to take larger prey items was likely also accompanied by less frequent feeding, a more sedentary lifestyle, and loss of the capacity to quickly flee. In contemporary lizards, those that are less active tend to have lower metabolic rates (Andrews and Pough 1985). As noted earlier, *Heloderma* has one of the lowest standard metabolic rates of any lizard (Beck and Lowe 1994). A more sedentary lifestyle likely evolved concurrently with a preference for drier, more seasonal habitats where an ability to subsist for long periods without feeding would have been particularly beneficial. The sporadic temporal availability of food resources in such environments reduces the demand for frequent activity. In such a scenario, the venom system could also have evolved in response to increased predation pressure as helodermatid ancestors became less active, slower, and more vulnerable to predators. The actual selection pressures may never be known, but it is likely that both protection from predators and prey acquisition played a role in the evolution of the venom system of the only extant venomous lizards.

The precursor of *Heloderma*'s venom apparatus, the Gland of Gabe, is also possessed by varanid lizards, yet no varanid lizard is known to be venomous [although some reptile keepers bitten by *V. griseus*, the Desert Monitor, have shown symptoms of toxicity (Ballard and Antonio 2001; chap. 3)]. Why are there no venomous varanid lizards? Venom is not needed for defense because most varanid lizards can quickly flee. Varanids have serrated teeth, an ability to tear flesh as they subdue prey, and some, such as *V. komodoensis*, have a highly infectious bite. An elaborate venom system may, therefore, not be necessary.

There are hundreds of species of venomous snakes; why are there not more venomous lizards? It appears that a unique combination of factors (perhaps selection for prey acquisition and defense, as discussed above) led to the evolution of only two species of venomous lizards. Snakes benefit greatly from a venom system because of their ability to quickly deliver venom during brief contact with their potentially dangerous prey, and because they swallow prey that are very large in proportion to their body size (Greene 1997). Because of the constraints inherent in the lizard body form, lizards have no choice but to bite and hold their prey in order to deposit venom effectively, and they generally take prey that is much smaller in relation to their own body size. The benefits of a venom system for prey acquisition, therefore, are greatly reduced. In the next chapter, we'll consider the venom system in more detail.

CHAPTER 3

The Venom System and Envenomation

THE MOST WIDELY recognized feature of the Helodermatidae family is that its members are venomous. Misunderstanding and confusion about this trait have accompanied *Heloderma* since before the genus was described by Hernández in 1577. As discussed in chapter 1, the specific epithet, *suspectum*, was chosen for the Gila Monster because E. D. Cope *suspected* it was venomous (Cope 1869), but it was not until well into the twentieth century that scientists agreed that, indeed, this was true. Debate continues over whether the venom is used for prey acquisition or defense, and, more recently, promise has arisen over its potential applications in modern medicine and pharmacology.

In this chapter, I outline the structure and function of the venom delivery system of helodermatid lizards. I provide a historical overview, synthesize recent developments in venom biochemistry, and consider the function of the venom system in its ecological context. I conclude the chapter with an overview of envenomation history and the treatment of bites.

HISTORICAL OVERVIEW

Several authors in the latter half of the nineteenth century commented on the "vile nature" of *Heloderma* and recognized that its unique grooved dentition might be associated with a venomous bite (see Bogert and Martín del Campo 1956). But it was not until the 1880s that the anatomy of the venom gland was investigated (Fischer 1882), and experiments were conducted to show that its salivary secretions were, in fact, toxic to other animals (Mitchell and Reichert 1883). Instead of resolving uncertainty about the venomous nature of *Heloderma*, however, this work served to initiate a controversy that lasted for several decades. Subsequent experiments (Yarrow 1888) failed to show toxic effects of *Heloderma* venom, probably because inappropriate methods were used to collect the venom. Additional investigators examined the histology of the venom gland (Holm 1897) and showed, with controls, that carefully extracted venom injected into small vertebrates had lethal effects (Santesson 1897; Van Denburgh 1898; Van Denburgh and Wight 1900). Nevertheless, skepticism remained. Snow (1906), having suffered a bite without experiencing serious pain or swelling, again raised the question of whether *Heloderma* was venomous. In 1907, Goodfellow made the following statement: ". . . exhaustive studies were made by some of the attaches of the Smithsonian Institution, among whom was Dr. R. E. Shufeldt, concerning the nature of the animal, and conclusions reached which the writer had previously attained—that the reptile was nonvenomous; and it may be accepted as conclusively demonstrated that the bite of the "monster" is innocuous per se. In 1913, an authoritative, 144-page book summarizing detailed studies of he venom of *Heloderma* was published by the Carnegie Institution of Washington (Loeb et al. 913). This book contained detailed studies by 11 contributors on numerous aspects of the venom, ncluding its biochemistry and effects on various physiological systems in a number of organ-sms. By the 1920s, this book, and additional studies on the venom gland, venom effects, and venom characteristics by Phisalix (1911, 1912, 917, 1922), finally convinced the scientific community that helodermatid lizards were indeed venomous, and the debate was settled over the "suspected" venomous nature of *Heloderma*.

VENOM DELIVERY SYSTEM

Heloderma delivers venom through an efficient system consisting of paired venom glands that empty through ducts at the base of venom-conducting teeth. Venom is produced and housed in multilobed venom glands (fig. 9), which, unlike those of venomous snakes, are located in the lower jaw and drain through ducts associated with each of the lobes. In contrast, he venom glands of snakes are situated behind he eye, above the upper jaw, and drain through a single duct that leads to an opening at the base of the associated fang (Greene 1997). The venom glands of *Heloderma* are not surrounded by compressor musculature as in most venomous snakes. Instead, tension within the glands produced by jaw movements propels venom toward the venom-conducting teeth, and capillary action carries the venom from grooved teeth into the wound.

The structure of the venom gland was first described by Fischer (1882), but the most complete descriptions to date remain the work of Fox (1913) and Phisalix (1912, 1917). More recent reviews (e.g., Bogert and Martín del Campo 1956; Tinkham 1971b; Russell and Bogert 1981), as well as what I provide below, are largely summaries of this earlier work.

The venom glands of helodermatid lizards are visible externally as conspicuous swellings below the lower lips (fig. 9, plate 20). Each gland is surrounded by a fibrous capsule from which septa extend to divide the gland into three or four distinct lobes (fig. 9). Each lobe of the venom gland is a structurally independent organ that forms a sac with a swollen glandular region at its base and a narrowed excretory duct near the upper end, which empties at the base of the teeth in the lower jaw (fig. 10). Each lobe of the venom gland is subdivided (by septa) into several lobules, which are further subdivided into smaller lobules. These subdivisions continue to occur, resulting in tiny chambers, or alveoli, each separated from one another by a delicate septum. The cavities within the alveoli are continuous with the lobules, which are, in turn, continuous with one another, forming a network of intralobular tubules. It is within these structures, apparently, that venom is produced by columnar, granule-secreting cells that line the intralobular tubules. As these cells discharge their contents, the secreted granules flow from the tubules into a central collecting lumen, which connects to the excretory duct. The lumen, along with associated tubules and alveoli, apparently also serves as a storage reservoir for venom.

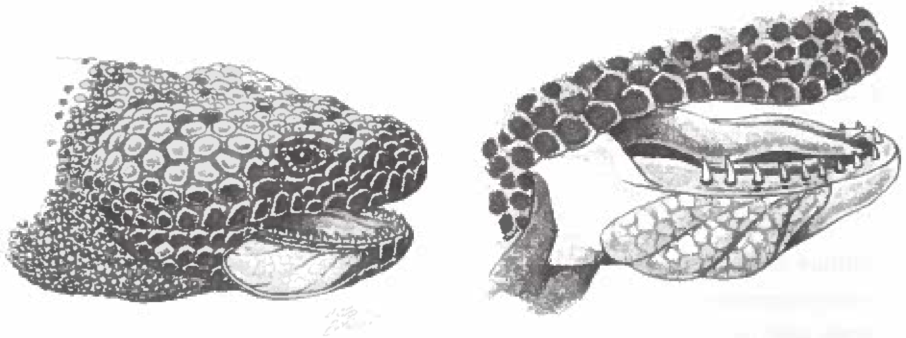


FIGURE 9. The venom glands of helodermatid lizards are located in the lower jaw. Each gland comprises three or four distinct obes as shown in these 2 views of a Gila Monster's right lower mandible with the skin removed (drawings by Randy Babb).

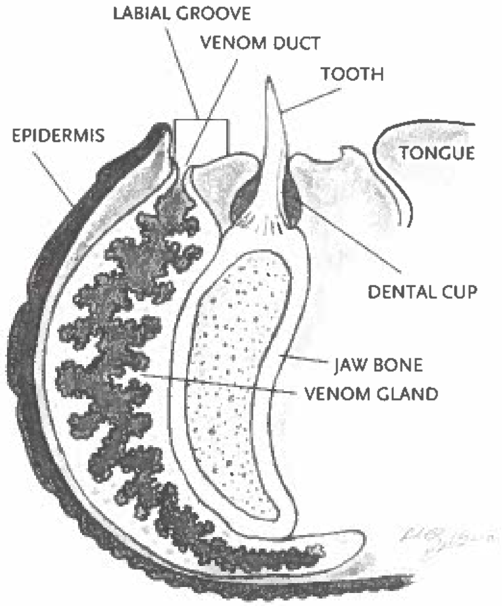


FIGURE 10. This cross section through the anterior portion of the right mandible shows relationships of the primary structures of the venom delivery system of helodermatid lizards. Each lobe of the venom gland forms a sac with a narrowed excretory duct near its upper end. The duct empties at the base of venom-conducting teeth in the lower jaw.

Helodermatids are not specialized for injecting large quantities of venom during brief contact, as are many venomous snakes, but the venom delivery system is structured to quickly and effectively transfer venom into a bite. During biting, tension produced in the gland by jaw movements propels venom through the venom ducts into a region between the fourth and seventh pair of dentaries (counting from the front), where the teeth show their greatest specialization for piercing and venom delivery. A series of small folds and grooves in the membranous tissue within this region serves as a temporary reservoir for the venom and may facilitate the flow of venom from duct to tooth. When the lizard bites, venom flows from these reservoirs through the grooved teeth into the wound.

Each specialized tooth has two grooves, with a shallower (sometimes absent) groove toward the rear (fig. 11) . Each groove is flanked by a cutting flange, which makes the tooth better adapted for piercing flesh than a merely conical tooth. Not all the teeth are similar in structure or size. The largest, most deeply grooved teeth are the dentaries (in the lower jaw), which can be up to 6 mm long in *H. horridum* and 5 mm long in *H. suspectum* (fig. 11). The maxillary

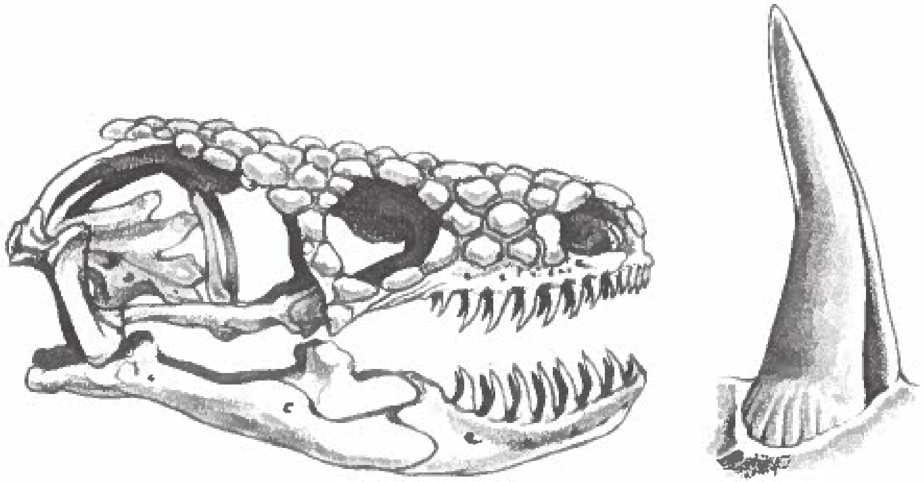


FIGURE 11. Skull of *Heloderma suspectum* showing arrangement of venom-conducting teeth (top). The largest, most deeply grooved teeth are the dentaries (in the lower jaw), which can be up to 5 mm long in *H. suspectum* (drawings by Randy Babb).

eeth (in the upper jaw) are shorter and less trongly grooved. Some teeth (especially the remaxillaries toward the front of the mouth) re hardly grooved at all, but they can still effectively deposit venom into an adversary (Tinkham 956; Strimple et al. 1997).

Jaw movements other than those associated vith biting may also produce sufficient tension vithin the glands to bathe all the teeth in enom. An agitated lizard will often display a lefensive posture of opening its jaws wide (exosing the purplish-white interior of its mouth) hen closing and reopening the jaws as a threat ontinues. This behavior may serve to bathe the naxillary teeth, dentaries, and premaxillaries in enom preparatory to envenomation.

The quantity of venom deposited into the victim may vary with many factors, including size of he lizard, degree of agitation, and length of time t remains attached. In captive Gila Monsters, uantities ranging from 0.5 to 2.0 ml in a single nilking have been extracted by a variety of methods (Loeb et al. 1913; Arrington 1930; Brown and owe 1955; Alagón et al. 1982; fig. 12).

FFECTS OF THE VENOM

he most complete investigation of the effects f *Heloderma* venom remains the work of Loeb t al. (1913) who tested hundreds of species, including invertebrates. Invertebrates are essenially immune to the effects of *Heloderma* enom. Effects on vertebrates are more severe nd varied. Ectotherms appear markedly less usceptible to the effects of the venom than do ndotherms (Cooke and Loeb 1913). Notably, ila Monsters appear to be immune to the efects of their own venom (Cooke and Loeb 1913; Brown and Lowe 1954).

In mammals, major effects include a rapid eduction in carotid blood flow followed by a marked fall in blood pressure, respiratory irregularities, tachycardia and other cardiac nomalies, as well as hypothermia, edema and internal hemorrhage in the gastrointestinal tract, lungs, eyes, liver, and kidneys (table 4). Common symptoms in dogs and cats include vomiting accompanied by discharge of urine and feces, and copious flow of saliva and tears. Death from large doses of *Heloderma* venom has been attributed primarily to respiratory disturbances (Cooke and Loeb 1913). Postmortem examinations reveal congestion and edema in the lungs, a marked congestion of the serous layer of the stomach and intestines, and hemorrhage in the kidneys and liver (Cooke and Loeb 1913; Ariano Sánchez 2003). Sublethal doses in mice and rats produce protrusion of the eyes and periorbital bleeding (Cooke and Loeb 1913; Ariano Sánchez 2003), and in rabbits they lead to an increase in the number of white blood cells (Meyers and Tuttle 1913). In humans, the effects of bites are associated with excruciating pain that may extend well beyond the area bitten and persist up to 24 hours. Other common effects of *Heloderma* bites on humans include local edema (swelling), weakness, sweating, and a rapid fall in blood pressure (see below). A summary of the effects of *Heloderma* venom on mammals is given in table 4.

The lethal dose (LD_{50}) of *Heloderma* venom varies among studies and venom lots (Russell and Bogert 1981). Such values are influenced by the relative amounts of venom and saliva collected in each sample and are, therefore, difficult to evaluate. The venom is most toxic when administered intravenously in mice, with LD_{50} values varying from 0.4 to 2.7 mg/kg for *H. suspectum* (table 5). With an i.v. LD_{50} of 1.4 to 2.7 mg/kg, the venom of *H. horridum* appears to have toxicity similar to that of *H. suspectum*. The LD for *H. horridum charlesbogerti* venom is 1.0 mg/kg when injected intramuscularly in rats (Ariano Sánchez 2003). When injected into mammals, the venom of *Heloderma* appears to be about as toxic as that of the Western Diamondback Rattlesnake, *Crotalus atrox* (Russell and Bogert 1981).

TABLE 4

Effects of Venom of Helodermatid Lizards in Nonhuman Mammals

EFFECTS	REFERENCES
Respiration	
Initial increase in rate, "forced" respirations followed by decrease and eventual standstill	Cooke and Loeb 1913
Ventilatory irregularities: gasping, rapid, shallow breaths, apnea	Patterson 1967a
Cardiovascular System	
Marked and rapid fall in blood pressure	Mitchell and Reichert 1883
Initial tachycardia	Van Denburgh and Wight 1900
Cardiac irregularities	Fleisher 1913
Impaired cardiac function/cardiac failure	Patterson 1967a
Reduction in carotid blood flow and arterial blood oxygenation	Russell and Bogert 1981
Cyanosis	
Hemorrhage	
GI tract	Cooke and Loeb 1913
Intestines, kidneys, lungs	Patterson 1967a
Eyes	Stýblová and Kornalik 1967
Liver	Ariano Sánchez 2003
Blood	
Leucocytosis	Meyers and Tuttle 1913
No effect on blood coagulation time	Cooke and Loeb 1913
Prolonged prothrombin time (anticoagulation)	Patterson and Lee 1969
Smooth Muscle	
Stimulating effect in ileum, colon, uterus	Patterson 1967b
Edema (note also with human envenomation)	
Intestines, stomach, lungs	Cooke and Loeb 1913
Other Effects	
Paralysis of limbs, partial paralysis of body	Patterson 1967a
Protrusion of eyes (exophthalmia)	Cooke and Loeb 1913
Lacrimation	
Abdominal rigidity	
Convulsions	
Vomiting	

NOTE: Based on in vivo studies in cats, dogs, guinea pigs, mice, and rats.

CHEMICAL MAKEUP OF THE VENOM

As knowledge of the toxic effects produced by *Heloderma* venom increased, so did interest in the chemical constituents causing these symptoms. The first studies on the chemical nature of *Heloderma* venom (Santesson 1897) identified two "toxic principles," referred to as *nuclein* and *albuminose*, but it was not until 1913 that the first toxin, a lipase, was isolated (Alsberg 1913). The 1960s saw renewed interest in the chemistry of *Heloderma* venom. Serotonin and amine oxidase activity were identified in the venom of *H. horridum* in 1960 (Zarafonetis and Kalas 1960). Mebs and Raudonat (1966) identified a very active hyaluronidase (a spreading factor; see below), phospholipase A, and a kinin-releasing enzyme with small proteolytic activity in both *H. horridum* and *H. suspectum* venom. In 1967, Tu and Murdoch showed that *H. suspectum* venom was largely a mixture of proteins, some of which hydrolyze

TABLE 5

LD$_{50}$ of Heloderma *Venom in Mice and Rats*

	AVENUE	SPECIES	LD$_{50}$ (MG/KG)	SPECIES
ohnson et al. 1966	Intraperitoneal	mice	3.0	*suspectum*
lebs and Raudonat 1966	Subcutaneous	mice	0.82	*suspectum*
tahnke 1966	Intraperitoneal	rats	10.3	*suspectum*
tahnke 1966	Intraperitoneal	mice	3.0	*suspectum*
atterson 1967a	Intracardiac	rats	1.35	*suspectum*
týblová and Kornalik 1967	Intravenous	mice	0.4	*suspectum*
týblová and Kornalik 1967	Subcutaneous	mice	4.0	*suspectum*
u and Murdock 1967	Subcutaneous	mice	2.0	*suspectum*
tahnke et al. 1970	Subcutaneous	rats	14.0–16.8	*suspectum*
Iendon and Tu 1981	Intravenous	mice	2.7	*suspectum*
ussell and Bogert 1981	Intravenous	mice	0.52	*suspectum*
lebs and Raudonat 1966	Subcutaneous	mice	1.4	*horridum*
Iendon and Tu 1981	Intravenous	mice	2.7	*horridum*
lagón et al. 1982	Intraperitoneal	mice	2.0	*horridum*
riano-Sánchez 2003	Subcutaneous	rats	1.0	*horridum* *charlesbogerti*

ertain peptides. Patterson and Lee (1969) ater showed coagulation was affected if enom was incubated with blood plasma for onger periods. Subsequent work isolated henorrhagic toxins in the venom (Nikai et al. 988; see below). In the late 1960s, Mebs isoated kallikrein from the venom of *H. suspecum* (Mebs 1968, 1969). Murphy et al. (1976) lemonstrated enzyme activities in the venom f *H. horridum*. In the 1980s, additional proeins—gilatoxin (Hendon and Tu 1981), horidum toxin (an arginine ester hydrolase; lagón et al. 1982; Nikai et al. 1988), helodernatine (a kallikrein-like hypotensive enzyme; lagón et al. 1986), an additional phospholiase (A$_2$; Gomez et al. 1989), and helothernine (Mochca-Morales et al. 1990)—were disovered and added to the known arsenal of *Ieloderma* venom components.

With the discovery in the 1980s that *Helolerma* venom contained strongly bioactive gents, with hormonelike actions similar to vaoactive intestinal peptides (VIP), interest and esearch in these intriguing molecules accelerted dramatically (Raufman 1996). Five bioacive peptides have been isolated so far from the venoms of Gila Monsters and Beaded Lizards: helospectin I and II (Parker et al. 1984), helodermin (Hoshino et al. 1984), exendin-3 (found in *H. horridum;* Eng et al. 1990), and exendin-4 (found in *H. suspectum;* Eng et al. 1992). These peptides mimic several human neurosecretory hormones that relax smooth muscle and mediate energy metabolism. The major compounds so far identified in the venom of helodermatid lizards as well as their chemical nature and physiological effects are discussed below and summarized in table 6.

HYALURONIDASE

Hyaluronidase is a hydrolase enzyme that cleaves internal glycosidic bonds of hyaluronic acid, a mucopolysaccharide that is an important component of connective tissue. Because this action facilitates venom diffusion into the tissue (Tu and Hendon 1983), hyaluronidase has been termed *spreading factor*. Hyaluronidase is also common in snake venoms where it also acts as a spreading factor (Meier and Stocker 1995). Venom of both *Heloderma* species shows particularly high hyaluronidase activity, which is believed to explain the potent edema effects of

TABLE 6

Major Constituents of Heloderma *Venom and Their Actions*

	DESCRIPTION/ACTION	PHYSIOLOGICAL EFFECTS
Hyaluronidase	Hydrolase enzyme; cleaves hyaluronic acid	Acts as a "spreading factor" by facilitating diffusion of venom through connective tissues surrounding bite site
Serotonin	Neurotransmitter hormone	Mediates inflammation, vasodilation, smooth muscle activity, and other effects
Phospholipase A$_2$	Hydrolase enzyme; catalyze hydrolysis of phospholipid glycerol backbone	Presynaptic membrane toxins in snakes; effects of *Heloderma* phospholipase A$_2$s are unknown
Nerve Growth Factor	Induce nerve growth; degranulate mast cells	Effects unknown
Helothermine	25-kDa peptide with similarity to family of mammalian cysteine-rich secretory proteins	Causes lethargy, partial paralysis of rear limbs, intestinal distension, and hypothermia in rats
Gilatoxin	33-kDa serine protease glycoprotein	Kallikrein-like lethal toxin; causes lowered blood pressure and contraction of isolated uterus smooth muscle in rats
Horridum toxin	31-kDa glycoprotein similar to gilatoxin	Kallikrein-like lethal toxin; causes hypotension, hemorrhage in internal organs, hemorrhage and bulging of the eyes
Helodermatine	63-kDa serine protease glycoprotein	Kallikrein-like enzyme; causes a dose-dependent decrease in arterial blood pressure in rats
Unnamed lethal toxin	28-kDa peptide	Kallikrein-like lethal toxin that suppresses contraction of isolated diaphragm muscle in mice
Helospectin I & II (exendin-1)	37- to 38-amino-acid peptides from exocrine gland having endocrine function	Stimulate amylase release from the pancreas; show physiological effects similar to VIP (vasoactive intestinal peptide); have been localized in various human tissues
Helodermin (exendin-2)	Basic 35-amino-acid peptide with stable secondary structure	Causes hypotension in dogs and rats; shows physiological effects similar to VIP
Exendin-3	39-amino-acid (4.2-kDa) peptide from *H. horridum* venom	Interacts with newly described exendin receptor and mammalian VIP receptors; induces amylase release from the pancreas
Exendin-4 (exenatide)	39-amino-acid peptide from *H. suspectum* venom	Induces insulin release through activation of glucagon-like peptide-1 (GLP-1) receptor
Gilatide	Fragment of exendin-4 peptide	Acts on GLP-1 receptor; improves memory in rodents

NOTE: See text for more complete descriptions and references.

eloderma bites (Mebs and Raudonat 1966; ussell and Bogert 1981).

EROTONIN

erotonin, derived from the amino acid tryptohan, produces potent local physiological efects and also functions as a neurotransmitter. erotonin mediates local processes such as inammation, vasodilation, and smooth muscle ctivity and causes aggregation of platelets Greger 1996). It is found in a variety of toxins rom animals such as spiders, toads, and wasps. he specific in vivo effects from the serotonin ound in *Heloderma* venom are not known, alhough it likely participates in the inflammation esponse.

HOSPHOLIPASE A_2

hospholipase A_2 enzymes are classified as hyrolases that act on ester bonds in fat molecules phospholipids). These common constituents f viperid and elapid snake venoms are toxic to resynaptic membranes, disrupting the release f neurotransmitters at nerve synapses and neuomuscular junctions and inhibiting platelets among other actions; Rosenberg 1988; Meier nd Stocker 1995). This behavior can cause aralysis and loss of muscle control and funcion, among other signs. We do not know hether phospholipase A_2 from *Heloderma* is esponsible for such actions in humans and ther mammals because the specific in vivo efects of this enzyme have not been investigated. However, phospholipase A_2 enzymes from *H. orridum* have been shown to inhibit platelet ggregation in human blood plasma (Huang nd Chiang 1994).

Five variants of phospholipase A_2 (or PLA_2) ave been identified and characterized in the enom of *H. suspectum* (Sosa et al. 1986; Gomez et al. 1989; Vandermeers et al. 1991). All of these stimulate the release of amylase rom secretory cells (acini) in rat pancreatic tissue, and they hydrolyze phosphatidylcholines lecithins), which are important in cell structure nd metabolism. Gila Monster PLA_2s are apparntly quite different from those found in snake venoms, especially in their N-terminal amino acid sequences and molecular weight (Tu 1991; Vandermeers et al. 1991). Interestingly, they are most similar to PLA_2 from bee venom. The major variant of PLA_2 in Gila Monsters (Pa5) shows a C-terminal extension seen only in *Heloderma* and bee *(Apis mellifera)* venoms (Gomez et al. 1989).

NERVE GROWTH FACTOR

Nerve growth factors are found in a number of viperid and elapid snake venoms. They normally induce the growth of nerve tissues, but they may also contribute to the toxic action of venoms by degranulating mast cells, which contributes to inflammation (Meier and Stocker 1995). A nerve growth factor was discovered in the venom of *H. horridum* in 1968 (Levi-Montalcini and Angeletti 1968), but its role remains unexplored.

HELOTHERMINE

This toxin from *H. horridum* venom is a 25.5 kDa protein with an N-terminal amino acid sequence initially thought to be unique (Mochca-Morales et al. 1990). Further characterization of helothermine showed it to have structural homology with a family of cysteine-rich secretory proteins found in mammalian male genital tracts and in salivary glands, as well as in some other animal toxins (Morrissette et al. 1995; R. L. Brown et al. 1999). When injected into mice, helothermine causes lethargy, partial paralysis of rear limbs, intestinal distension, and lowering of body temperature; hence, as its name suggests, it is a potentially hypothermic toxin (Mochca-Morales et al. 1990). Although deadly to mice, its LD_{50} has not been reported (Mochca-Morales et al. 1990). Helothermine blocks certain ion channels in cell membranes (e.g., calcium channels in cardiac muscle, skeletal muscle, and cerebellar granules; Morrissette et al. 1995; Nobile et al. 1994, 1996). This property gives it promise as a pharmacological tool for studies on the structure and function of ion channels in muscle and brain tissue. Unlike other toxins found in the venoms of helodermatid lizards (discussed below), helothermine shows no enzymatic effects. Helothermine is a member of the helveprins (20–25 kDa proteins), which are found in many reptile venoms (S. P. Mackessy, pers. comm.).

THE KALLIKREIN-LIKE TOXINS

These are the toxins most responsible for the excruciating pain that results from the bites of Gila Monsters and Beaded Lizards. Four different proteins that possess kallikrein-like toxins have been identified in the venom of helodermatid lizards (table 6). Kallikreins are hypotensive hormones that exert powerful local physiological effects. They cleave kinogens that, in turn, release bradykinins—local hormones that mediate the inflammation/pain response. Bradykinins produce pain by stimulating both sensory C-fibers and spinal ganglia, and they reduce blood sugar by shifting D-glucose from plasma to muscle (Greger 1996). Bradykinins also cause vasodilation of peripheral arterioles and increased vascular permeability, which results in edema (swelling caused by leaking of plasma fluid into tissues). Bradykinins also stimulate secretion of adrenaline, which can cause an increase in heart rate, among other effects. Plasma concentrations of bradykinins are usually very low (4 pmol/L) so local increases in these substances can have dramatic effects (Greger 1996). Kallikreins in venoms of viperids may contribute to the immobilization of prey animals (Meier and Stocker 1995).

As with helothermine, above, the first three kallikrein-like proteins have been shown to be lethal toxins.

GILATOXIN

Gilatoxin, a glycoprotein, was the first lethal toxin isolated from the venom of helodermatid lizards (Hendon and Tu 1981). Later research found that gilatoxin is one of several toxins in *Heloderma* venom that shows kallikrein-like activity (Utaisincharoen et al. 1993). Present in both species, it comprises about 3%–5% of the venom volume. Gilatoxin is a serine protease that acts on a number of substrates including kininogen and angiotensin, which are involved in mediating blood pressure. Gilatoxin appears to be found only in helodermatid lizards and has an LD_{50} of 2.6–2.9 μg/g. Interestingly, it becomes more toxic when administered to mice in combination with other venom fractions (Tu 1991), suggesting that the toxin acts synergistically with additional venom components.

HORRIDUM TOXIN

Horridum toxin, from the venom of *H. horridum*, is the only hemorrhagic toxin so far isolated from helodermatid lizards. Another glycoprotein, horridum toxin is a distinct form of gilatoxin, but with a similar structure (Nikai et al. 1988; Datta and Tu 1997; Tu 2000). It also shows kallikrein-like activity, releasing bradykinin upon hydrolysis of kinogen (Datta and Tu 1997). Similar to gilatoxin, it has strong hypotensive effects when injected into rats. It is more toxic than gilatoxin, showing an LD_{50} of 0.38 μg/g (Nikai et al. 1988). In addition to the inflammatory effects produced by bradykinin, horridum toxin causes hemorrhage in internal organs and especially in the eye, leading to exophthalmia (protrusion of the eyeballs), an effect that has not been observed from other venoms (Datta and Tu 1997). The actual exophthalmic effect, however, occurs only when the kallikrein activity is contaminated with a similar-sized metalloprotease (S. P. Mackessy, pers. comm.). Although horridum toxin has been isolated only from *H. horridum*, exophthalmia has also been observed in rats and mice injected with venom from *H. suspectum* (Cooke and Loeb 1913; Patterson 1967a; Stýblová and Kornalik 1967), suggesting a similar toxin may also be present in the venom of the Gila Monster. Horridum toxin has been shown to degrade fibrinogen to fibrin, an important step in the blood coagulation process that is normally performed by the enzyme thrombin. Clots do not form from horridum toxin poisoning, however, suggesting that it does not act like thrombin, as do many snake venoms that show kallikrein-like activity.

UNNAMED LETHAL TOXIN

Another very toxic "lethal toxin" was isolated from the venom of *H. horridum* by Komori et al. (1988). This toxin has a molecular weight of 28 kDa and an LD_{50} of 0.135 $\mu g/g$ when injected intravenously in mice. This appears to be the most toxic substance isolated so far from the venom of *Heloderma*. The toxin suppresses contraction of the diaphragm muscle in mice, but shows no hemolytic or hemorrhagic activity. Proteolytic, phospholipase A_2, or arginine ester enzymatic activity are all absent in this apparently novel toxin (Kamori et al. 1988).

HELODERMATINE

Not considered a lethal factor, helodermatine is an arginine esterase purified from *H. horridum* venom. It was the first enzyme with kallikrein-like activity to be isolated and characterized from *Heloderma* venom (Alagón et al. 1986). Helodermatine is another serine protease glycoprotein, as are gilatoxin and horridum toxin, but, at 66 kDa, it is about twice their molecular mass. When injected into anesthetized rabbits, it causes a rapid dose-dependent decrease in arterial blood pressure, an effect likely attributed to its active kallikrein nature. Its N-terminal amino acid sequence is similar to kallikrein from pig pancreas and to kallikrein-like enzymes from venom of the rattlesnakes *Crotalus atrox* and *C. adamanteus*.

THE BIOACTIVE PEPTIDES

In the early 1980s, investigators searching for biologically active chemicals in animal venoms made a very important discovery. They found that the venom of helodermatid lizards elicited a spectacular secretory response from pancreatic acini (secretory cells that make a useful model system for testing the biological activity of chemical substances; Raufman 1996). This discovery led to an intense effort to find the compounds responsible for this response, which culminated in 1984 with the description of helospectin I and II (Parker et al. 1984) and helodermin (Hoshino et al. 1984). These peptides are similar in structure and action to VIP (vasoactive intestinal peptide), a hormone secreted by nerves found throughout the gastrointestinal tract. A neurotransmitter hormone, vasoactive intestinal peptide is a powerful relaxant of smooth muscle (hence its name) and mediates the secretion of water and electrolytes by the small and large intestines. (Interestingly, VIP-secreting tumors give rise to "pancreatic cholera" with symptoms similar to those shown by a severe bite case—see below.) The actions and structure of VIP are also similar to secretin, another messenger peptide involved in stimulating pancreatic secretions. In the early 1990s, two additional biologically active peptides, exendin-3 and exendin-4, were discovered in the venom of helodermatid lizards (Eng et al. 1990, 1992). Exendins are so named because they are peptides from *ex*ocrine glands (of *Heloderma*) having *end*ocrine actions (Eng et al. 1990). The helospectins became known as exendin-1 and helodermin as exendin-2.

Exendins (including helospectins and helodermin) exert their biological effects by interacting with specific receptors found on cell membranes in various tissues of mammals. The receptors known to be involved include VIP and secretin receptors, exendin receptors (newly discovered because of work with *Heloderma* venom), and GLP-1 receptors (involved in insulin release and glucose metabolism). The effects of these bioactive peptides are numerous and diverse, but they generally involve decrease of blood flow via effects on smooth muscle, and activation of adenyl cyclase. Adenyl cyclase, an enzyme released when a mammal requires energy, catalyzes a reaction that results in the formation of cAMP, which, in turn, activates numerous enzymes including those that metabolize carbohydrates for energy production. An excellent review of bioactive peptides from *Heloderma* is given in Raufman (1996). The nature and action of these interesting peptides are discussed below.

THE HELOSPECTINS

Helospectin I and II are very similar peptides (38 and 37 amino acids, respectively) that stimulate amylase release from the pancreas. Helospectin I differs from helospectin II in that it has an additional serine residue at its C terminus. It is believed that, because of their similar actions, helospectins and VIP act on a common membrane receptor in mammals (Grundemar and Hogestatt 1990). Six forms of helospectin have recently been identified from *H. horridum* venom that show minor differences in the side groups attached to their Ser32 residues (Vandermeers-Piret et al. 2000). Interestingly, helospectins (and helodermin) have been immunohistochemically localized, usually associated with nerve endings, in a variety of human tissues ranging from the upper respiratory tract to the genitalia (Graf et al. 1995; Hauser-Kronberger et al. 1996, 1999). In these tissues, they appear in association with VIP receptors and (as with VIP and secretin) may play a role in regulating secretory activities and local blood flow. The location of these lizard venom peptide sequences within the tissues of mammals leads to some intriguing ecological and evolutionary questions (see below). The helospectins are present in venoms of both *H. horridum* and *H. suspectum*, but they are more abundant in *H. horridum* venom.

HELODERMIN

Helodermin, a basic 35-amino-acid peptide discovered in Gila Monster venom, was the first secretin/VIP-related peptide found in an animal other than a mammal or bird (Hoshino et al. 1984; Vandermeers et al. 1984). In dogs, it causes prolonged, systemic hypotension (Robberecht et al. 1988); in rats, it produces a dose-dependent hypotension, apparently via K^+ channels that exist on arterial smooth muscle cells (Horikawa et al. 1998). The discovery of helodermin also included the discovery of another bioactive peptide, pancreatic secretory factor, that later turned out to be a member of the phospholipase A_2 family (Dehaye et al. 1984; Vandermeers et al. 1984). In comparison with other members of the secretin/VIP family of peptides, helodermin has an unusually stable secondary structure, partly owing to a secondary configuration it maintains in water, which may account for its prolonged physiological action (Blankenfeldt et al. 1996). Helodermin shows 85% identity with helospectin I and II, which probably explains the similarity in their biological activity (Raufman 1996) and also suggests a common evolutionary origin for these venom peptides. Helodermin binds to receptors in a number of human tissues in the gastrointestinal tract, lungs, and even on human breast cancer cells (Raufman 1996). It has also been shown to inhibit growth and multiplication of lung cancer cells (Maruno and Said 1993). Helodermin may also inhibit the activity of phospholipase A_2, suggesting that it could serve a protective function to attenuate phospholipase activation within the venom glands (Raufman 1996). Helodermin is found only in the venom of *H. suspectum*.

EXENDIN-3 AND EXENDIN-4

The most important peptides in *Heloderma* venom, in terms of pharmacological applications, are exendin-3 and exendin-4. Exendin-3, a 39-amino-acid peptide, occurs in the venom of *H. horridum*. It shows similarity with other hormones involved in digestion: glucagon (48%) and human glucagon-like peptide-1 (GLP-1; 50%). In its 12 amino acid residues, it has strong homology with secretin (91%), but only 41% with secretin overall, and only 29% similarity to VIP. It shows limited structural similarity with helospectin and helodermin (32% and 26%, respectively; Eng et al. 1990).

Exendin-4, found only in Gila Monster venom, differs from exendin-3 by two amino acids, suggesting minor evolutionary changes from an ancestral peptide (Raufman 1996). Exendin-4 shows great structural homology (53%) to human glucagon-like peptide-1, a hormone released from the gut in response to a meal (Goke et al. 1993; Raufman 1996; Drucker 2001). GLP-1 stimulates insulin release and moderates blood glucose levels, traits that have attracted interest in its potential for treating Type II (noninsulin dependent) diabetes (Goke et al. 1993; Doyle and Egan 2001). In the blood, GLP-1 has a short half-life and must, therefore, be administered frequently to maintain adequate insulin levels. Exendin-4, on the other hand, activates the same receptor as GLP-1 but turns out to be more effective at inducing insulin release. Moreover, exendin-4 has a much longer biological action than GLP-1 (Young et al. 1999a; Doyle and Egan 2001). Amylin Pharmaceuticals, Inc., has developed a synthetic exendin-4 (AC 2993) that lowers plasma glucose to within the normal range, without inducing hypoglycemia, in people with Type II diabetes (Kolterman et al. 1999, 2003). In healthy volunteers, exendin-4 also reduces plasma glucose by delaying gastric emptying and by reducing calorie intake (Edwards et al. 2001).

These traits have propelled exendin-4 to the forefront of pharmacological research on the treatment of diabetes. A search of the medical literature for exendins will turn up hundreds of papers published since their discovery in 1990. Adult-onset (Type II) diabetes accounts for most of the 17 million cases of diabetes in the United States. Prospects for exendin-4, or its trade name exenatide (AC 2993), currently in phase 3 development for use in treating human diabetes, are so bright that Eli Lilly & Company closed a $325 million deal in September 2002 with Amylin Pharmaceuticals for rights to develop and market a synthetic version of this compound (fig. 12).

GILATIDE

This novel nine-amino-acid peptide, discovered in 2001, is really a fragment of the larger exendin-4 molecule (Haile et al. 2001, 2002). The extent to which it occurs independently in the venom of helodermatid lizards is not yet

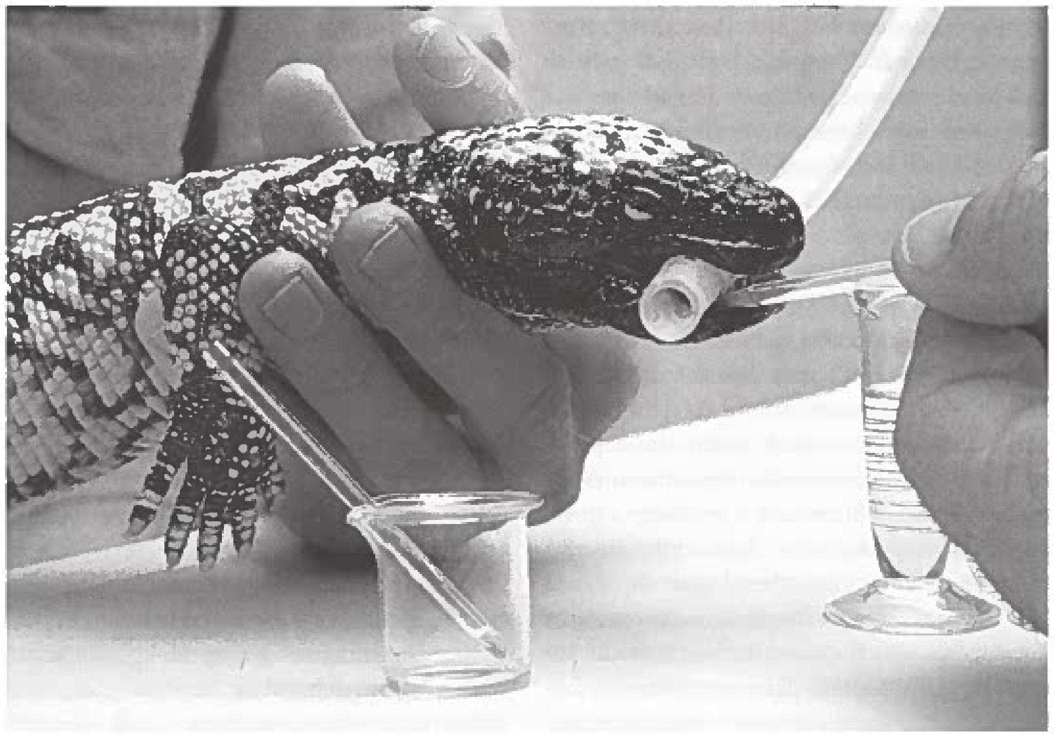


FIGURE 12. The venom of helodermatid lizards also contains several bioactive peptides that have brought the shy, venomous lizards into pharmacology journals and headlines in medicine. The best-known lizard peptide, exendin-4, mediates insulin release and glucose uptake from the blood after a meal. A synthetic version of exendin-4 (exenatide) is a leading candidate for treating adult-onset (Type II) diabetes, which accounts for most of the 17 million cases of diabetes in the United States. Prospects for this drug are so bright that Eli Lilly & Company recently closed a $325 million deal with Amylin Pharmaceuticals for rights to develop and market this compound (photo by Tom Wiewandt).

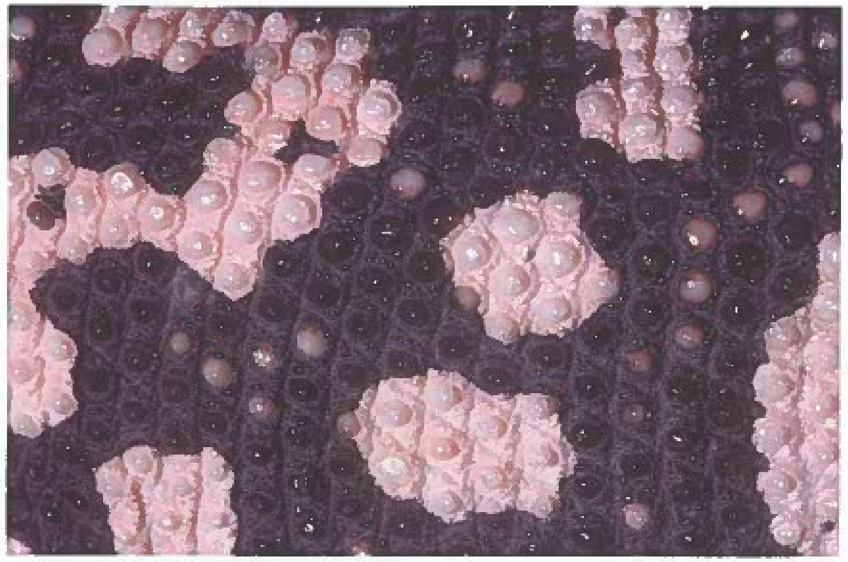
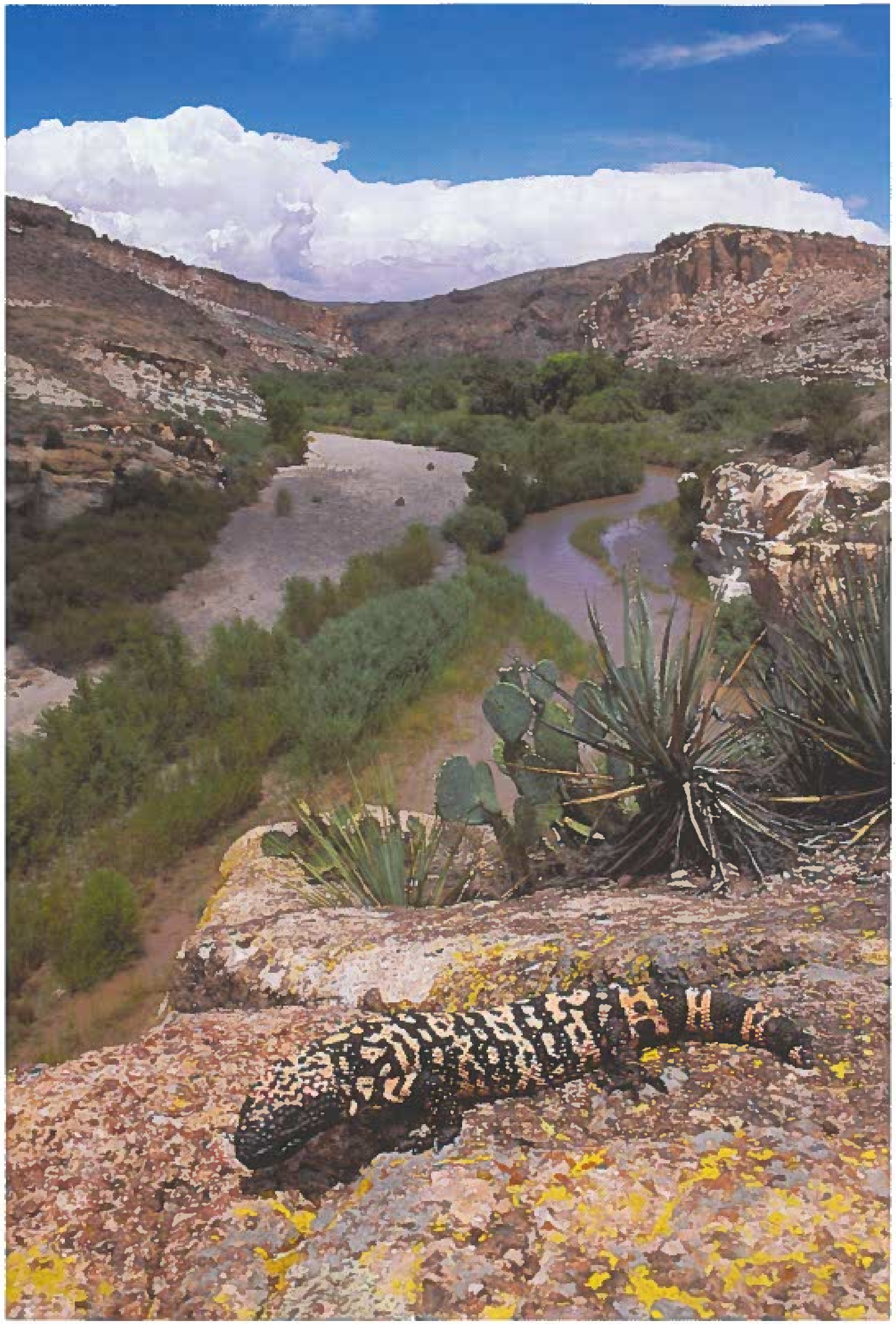


PLATE 1. The genus *Heloderma* was derived from the Greek words *helo* for "nail stud" and *derma* for "skin," terms which describe the bumpy osteoderms (bone-impregnated scales) shown in this photograph, which cover much of the body of helodermatid lizards.

PLATE 2. As with most Beaded Lizards, *Heloderma horridum alvarezi* (pictured here), prefer tropical dry forest habitats and spend far more time in trees than do Gila Monsters. The large forked tongue (red in *H. horridum*, but black in *H. suspectum*) is an important chemosensory organ used for finding food, shelters, and potential mates.



LATE 3. The Gila Monster was named after the Gila River, which flows from southwestern New Mexico, where this photo-
raph was taken, through southern Arizona.

PLATE 4. Helodermatid lizards are at once cryptic and aposematic. Their mottled patterns mingle with the broken shadows and textures of their desert and tropical dry forest habitats.

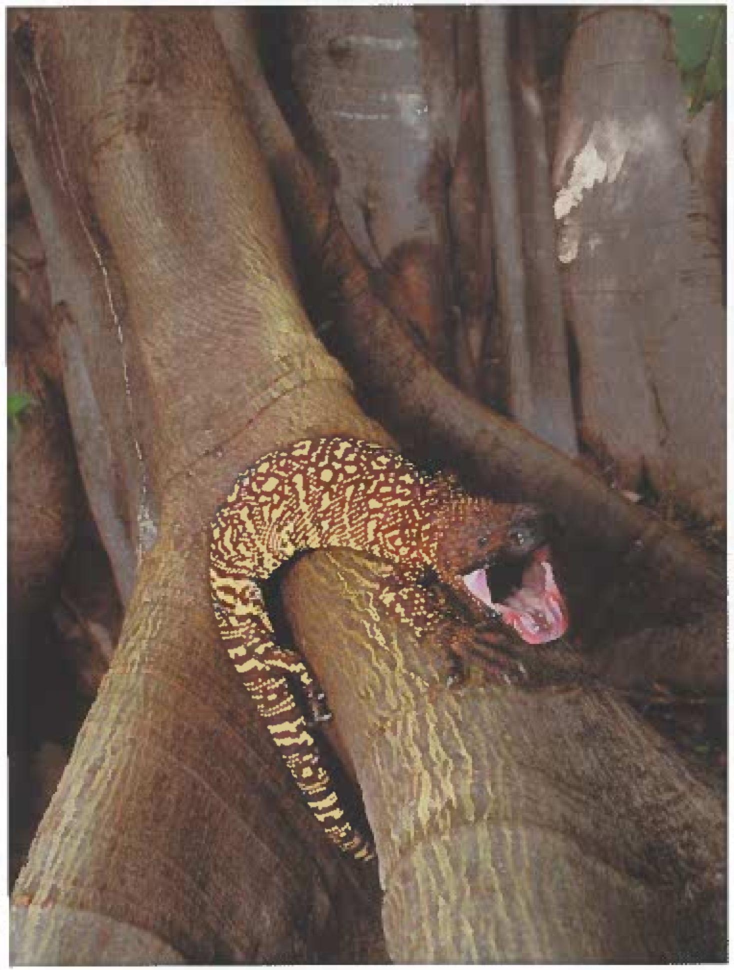
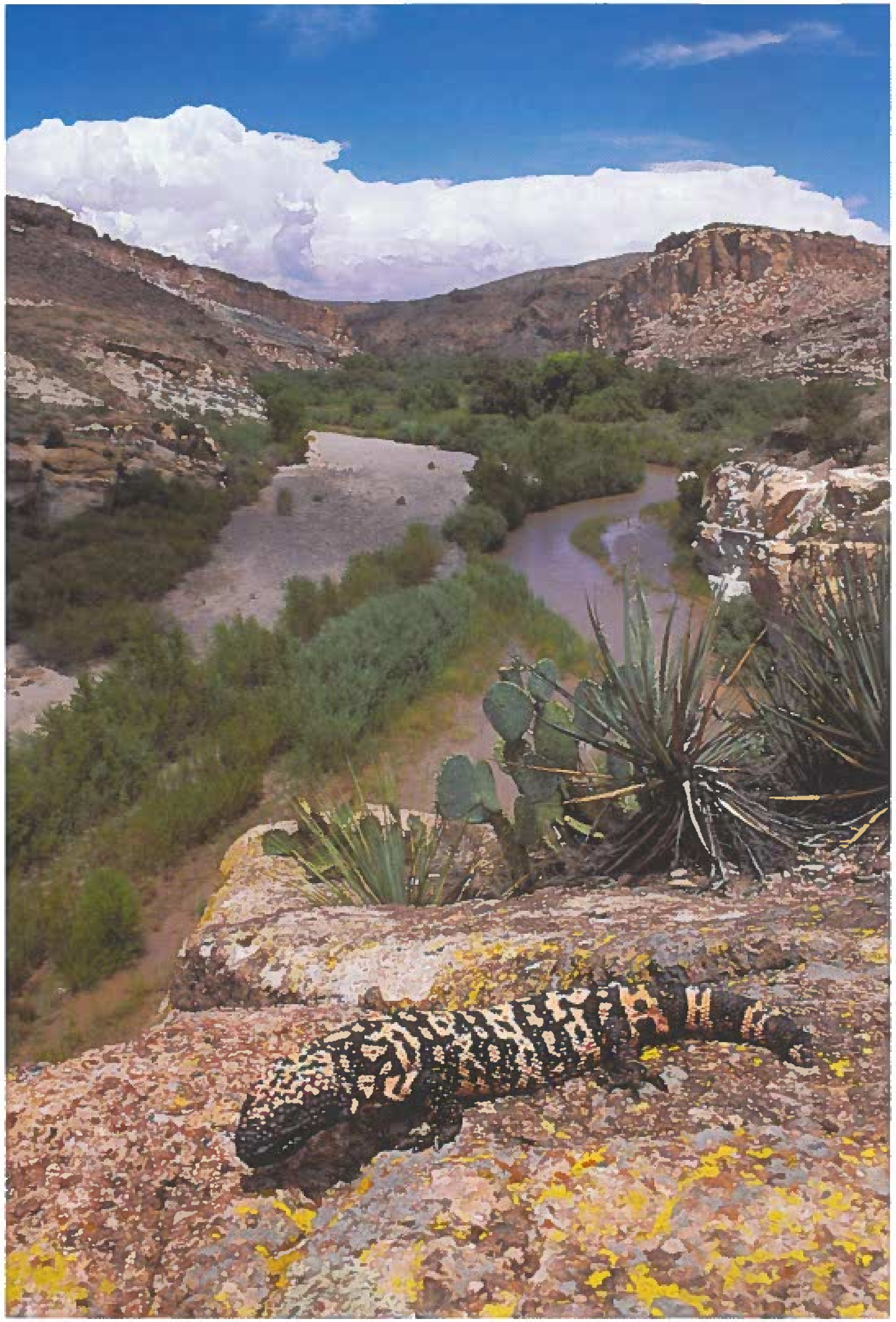


PLATE 5. Approach more closely and camouflage is transformed into a bright, bold BEWARE: a wide-open mouth—soaked in venom—hisses a warning that a very nasty bite awaits those who advance further.



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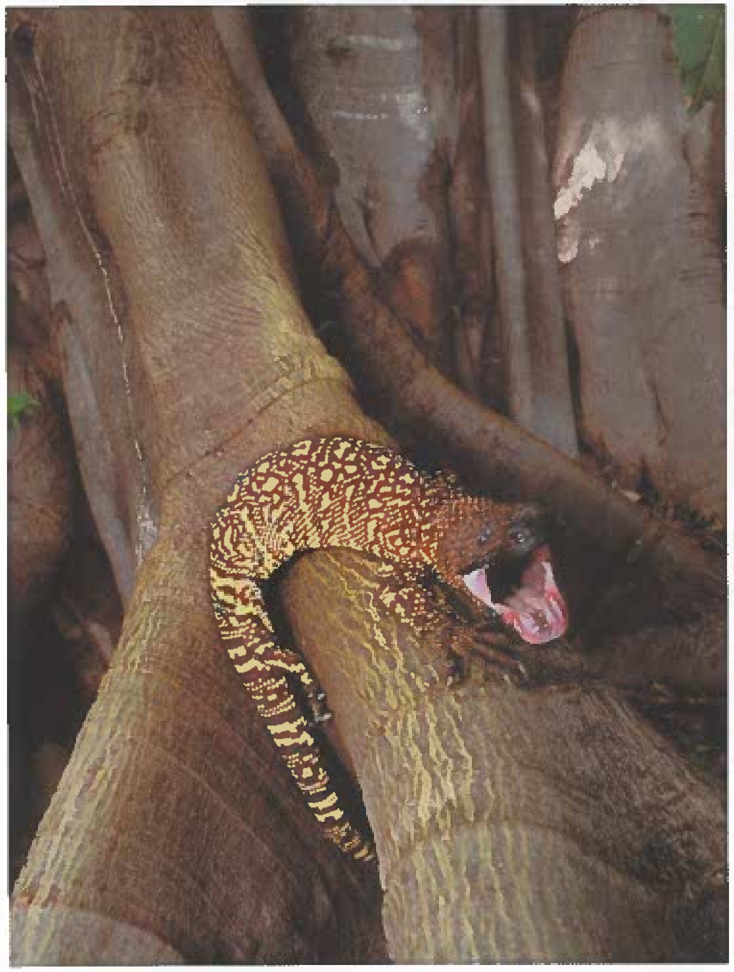
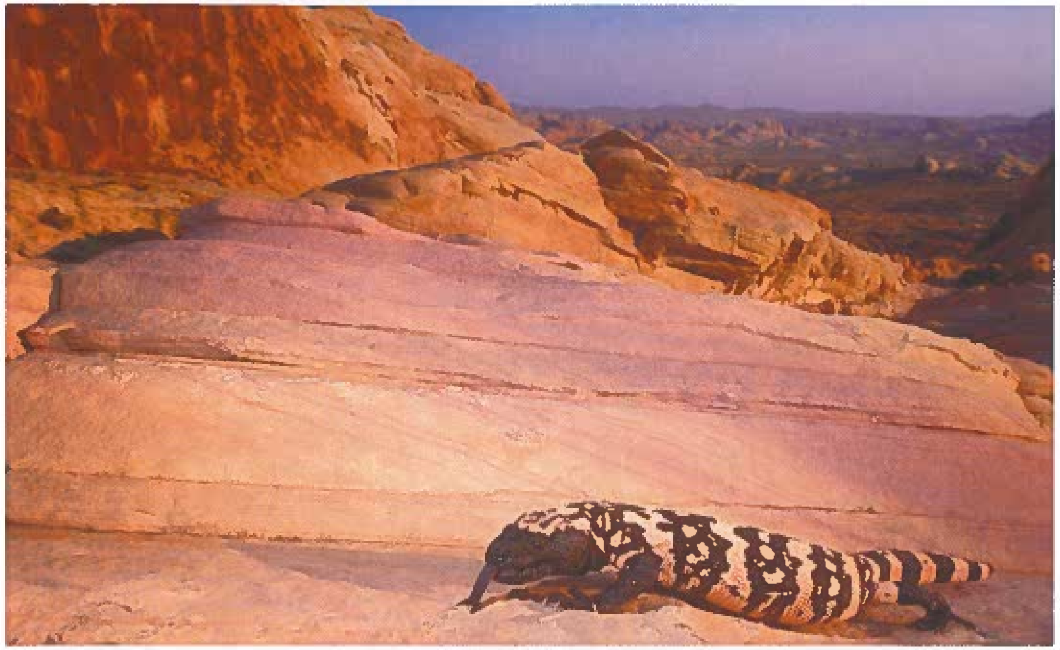


PLATE 5. Approach more closely and camouflage is transformed into a bright, bold BEWARE: a wide-open mouth—soaked in venom—hisses a warning that a very nasty bite awaits those who advance further.

ATE 6. Helodermatid lizards are members of an ancient clade, the Monstersauria. Shown here is *Estesia mongoliensis*, a onstersaur that inhabited Mongolia 77 million years ago. Like *Heloderma*, *Estesia* had venom grooves on its teeth. Its bones ve been found alongside protoceratopid dinosaur nests, prompting the paleontologists who discovered the fossil to propose e dramatic scenario depicted here (courtesy of the American Museum of Natural History).



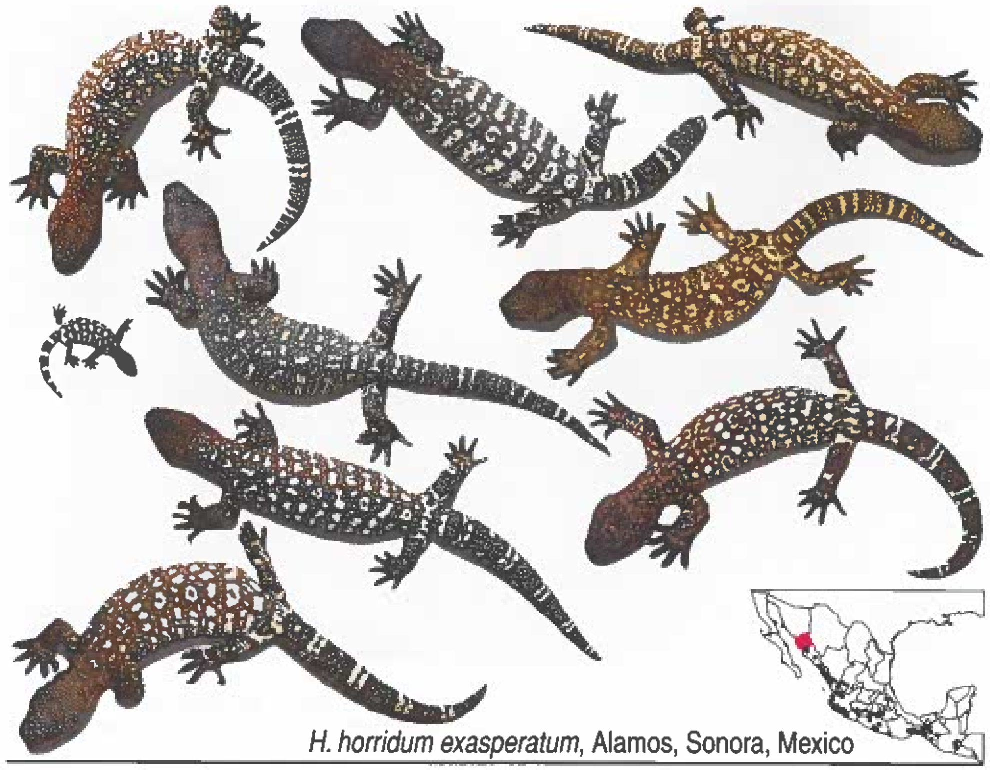
PLATES 7 AND 8. In quest of a nest. . . . Foraging Gila Monsters and Beaded Lizards take advantage of favorable surface conditions in sometimes-harsh environments to locate the hidden nests of vertebrates, whose eggs and young they feed upon. The Gila Monster (above) is from the Mohave Desert, and the Beaded Lizard (below) has just discovered a dove nest in a tropical dry forest of southern Sonora, Mexico.

PLATE 9. In a new twist on lizard behavior, we see here male helodermatid lizards vying for access to females by performing spectacular combat rituals, reminiscent of the entwining combat dances of snakes. These tests of dominance may continue for hours, pushing the combatants' physical abilities to the limit. Males with greater endurance may more frequently emerge victorious during combat rituals and thereby enjoy greater reproductive success. The entwining postures occurring with both Gila Monster and snake combat provide a telling glimpse at the evolutionary ties between the two groups.

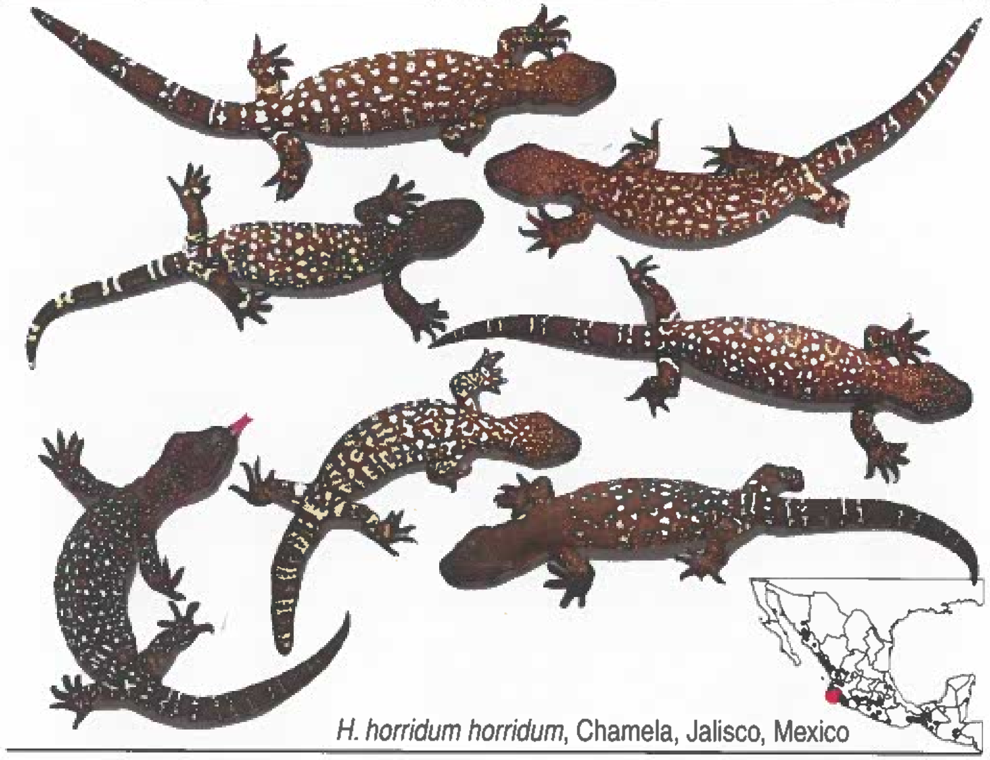
PLATE 10. Hatching may take several days as hatchlings absorb remaining yolk, which can make up over half the egg mass. After hatching, Gila Monsters spend weeks, even months, in or near the nest, making the absorbed yolk a crucial energy source for the first months of life. Hatching, simulated here in captivity, has yet to be witnessed in nature. Debate continues over whether eggs hatch in fall or in spring after overwintering in the nest (photo by Tom Wiewandt; eggs courtesy of Mark Seward).

PLATE 11. Among the greatest threats to Beaded Lizards and Gila Monsters are habitat loss and fragmentation. Tropical dry forests are being cut to accommodate expanding agricultural (such as the agave plantation shown here) and tourist development.

PLATE 12. Desert habitats around St. George, UT (seen here), where Gila Monsters were once abundant, are giving way to one of the fastest-growing retirement communities in the United States.



H. horridum exasperatum, Alamos, Sonora, Mexico



H. horridum horridum, Chamela, Jalisco, Mexico

PLATE 13. Portraits of populations: These photographs show a typical range in variation of dorsal patterns within populations of two subspecies of Beaded Lizards. Note the higher degree of speckling on tails of *H. h. exasperatum* (top) in comparison with *H. h. horridum* (bottom).

known. Gilatide has been shown to strongly enhance memory in mice, based on standard cognition tests. This effect appears to be mediated through GLP-1 receptors, a pathway previously unknown to be involved in learning and memory (Haile et al. 2002). Anonyx, a New York–based pharmaceutical company, is investigating the potential for using gilatide to help people suffering from memory disorders such as those associated with Alzheimer's disease and attention deficit/hyperactivity disorder (ADHD). Should gilatide indeed turn out to be an active, independent component of helodermatid lizard venom, what could be a more effective formula for a defensive venom than to mix components producing great pain with one that also enhances one's memory of the experience?

A summary of the major constituents of *Heloderma* venom is provided in table 6. Many of these peptides have valuable research and pharmacological applications. Venom constituents have enabled discovery of new membrane receptors in mammals, have enlightened physiologists as to how these receptors function, and hold promise for treating diseases such as cancer and diabetes. The venom of helodermatid lizards may be unique among reptile venoms in showing such a high number of bioactive peptides (Bertanccini 1976; Raufman 1996). Why do several venom constituents closely resemble human neurosecretory hormones? Why does the venom exhibit a redundancy of peptides producing strong kallikrein-like activity? What is the ecological function of this complex slurry of peptides, and how do the various venom components act to achieve their ecological role, if any? The answers to these questions are best considered in an ecological and evolutionary context.

ECOLOGICAL/EVOLUTIONARY ROLE OF HELODERMATID VENOMS

Although the biochemistry of *Heloderma* venom shows great promise in pharmacology, its ecological role has received less attention. A perennial source of confusion has been whether the venom system of *Heloderma* is used primarily for defense, or to subdue and aid in digesting prey, as is the case for most venomous snakes. In snakes, venom serves an important feeding role, primarily in subduing or immobilizing prey that are large, dangerous, or otherwise difficult to handle (Greene 1997). Most vipers immobilize their prey by rapidly injecting large quantities of toxins that induce hypotension, clotting, and the enzymatic breakdown of tissues, especially the lining of blood vessels (Meier and Stocker 1995; Greene 1997). Many elapid snakes (e.g., cobras and mambas) inject smaller quantities of neurotoxins that immobilize prey by blocking impulses at the neuromuscular junction, paralyzing muscles of respiration and leading to respiratory failure (Greene 1997). Many snake venoms have both tissue-destructive and neurotoxic properties. A secondary feeding role of snake venoms may be to aid in digesting prey, although few studies have directly demonstrated this effect (Thomas and Pough 1979). Predigestion may be particularly important for viperids that inhabit cooler temperate latitudes and feed on relatively large prey (Thomas and Pough 1979; Mackessy 1988; Greene 1997). In contrast to most venomous snakes, effects of envenomation by *Heloderma* tend to be more localized and, as summarized above, show relatively little tissue destruction.

Thus the utility of snake venoms for defense, although often profound, is secondary to their feeding role (Greene 1997). For helodermatid lizards, on the other hand, an elaborate venom system seems unnecessary for subduing prey. Beaded Lizards and Gila Monsters are specialized nest predators that feed almost entirely on eggs or juvenile birds and mammals (see chap. 7). Venom is not needed to subdue defenseless young or eggs in vertebrate nests. Helodermatid lizards do not feed on rapidly moving prey, and, although meals may be large, individual prey tend to be smaller than 10% of their adult body mass. The venom system of *Heloderma* precludes rapid injecting of venom during brief contact, a trait that is important for subduing large prey that are dangerous and difficult to handle. Moreover, the venom of helodermatid lizards does not appear to have sufficient tissue-destroying properties to be effective in helping to predigest prey (see above).

Nor do limited field observations suggest the use of venom to subdue prey. Wild Gila Monsters feeding on juvenile cottontails (relatively large prey at approximately 45 g each) delicately swallow the nestlings without the characteristic chewing or pumping motions shown when envenomating an adversary (Beck 1990; chap. 7). In captivity, however, I have observed Gila Monsters and Beaded Lizards that were feeding on dead mice "chewing" their prey before swallowing them. Although these observations do not rule out a feeding function, they suggest that the venom of helodermatid lizards does not serve a major role in subduing prey. In some cases, however, especially for juveniles, it could aid in immobilizing prey.

A digestive role of the venom might be ruled out entirely were it not for exendin-4, which comprises up to 5% of the dry weight of Gila Monster venom (J. Eng, pers. comm.) and has been shown to increase 30-fold in the blood of Gila Monsters immediately after a meal (Young et al. 1999b). This result leaves open the intriguing possibility that exendin-4 could regulate glucose uptake in the gut of helodermatid lizards. Could the venom glands, which are modified salivary glands, serve as a source of hormones exerting endocrine control of carbohydrate metabolism in Gila Monsters and Beaded Lizards? We do not yet know what physiological role, if any, exendin serves in *Heloderma*. It remains to be discovered, or discounted, whether exendin might aid in lizard digestion just as it may help humans cope with diabetes. So, whereas it seems obvious that helodermatid lizards need not use venom to subdue their prey, a role of the venom system in processing prey remains a possibility that needs to be further explored (chap. 10).

For defense, on the other hand, the venom system is crucial. Gila Monsters and Mexican Beaded Lizards spend the vast majority of their time hidden in shelters, yet they occasionally travel considerable distances during infrequent aboveground forays (Beck 1990; Beck and Lowe 1991). These large, slow-moving lizards cannot quickly sprint away from a potential threat, as can most other lizards. Their peak speed of 1.7 km/hour on a treadmill (Beck et al. 1995) contrasts strikingly with some inguanine lizards of similar size, which can attain speeds of over 25 km/hour (Garland 1984). These traits make surface-active *Heloderma* particularly vulnerable to predators. Predation is obviously an important factor, and *Heloderma* occasionally succumb to predators (see chap. 6).

Gila Monsters and Beaded Lizards generally avoid encounters with predators by relying on their secretive habits and cryptic patterns. While radiotracking surface-active Beaded Lizards in Jalisco, I often observed that, when lizards noticed my presence from a distance, they would stop moving and press their body to the ground. As I approached more closely, Beaded Lizards (and Gila Monsters) attempted to escape but could be easily overtaken and captured if they could not quickly flee into a burrow. Thus, when confronted with an adversary during an aboveground foray, the inability of *Heloderma* to swiftly escape necessitates an effective defense.

How effective is the bite of *Heloderma* at repelling potential predators? As an adversary is seized by the jaws of a heloderm, a complex mixture of venom proteins and peptides also seizes physiological control of the intruder. Kallikrein-releasing toxins cause immediate bradykinin release accompanied by severe pain, inflammation, weakness, and a rapid drop in blood pressure. Hyaluronidase enzymes facilitate the spread of venom components through connective tissues surrounding the bite site. Horridum toxin may begin causing internal hemorrhaging; helothermine may begin acting to lower body temperature and induce lethargy.

Meanwhile, the heloderm holds on with bulldog tenacity and continues to chew additional venom into the wound. At this point, all of an intruder's attention must be focused on removing the venomous lizard from the bitten area. And herein lies another of the paradoxes of helodermatid lizards. The same behavior that so effectively delivers venom to its enemies (and makes them wish they had avoided contact to begin with) puts the lizard at risk of injury as an adversary attempts to remedy its painful situation.

How can this apparent paradox be resolved? Is the effectiveness of *Heloderma*'s venomous bite really undermined by its tenacious behavior? There are very few recorded accounts of direct encounters between *Heloderma* and their natural predators (Sullivan et al. 2002; chap. 6). Of 12 cases of Gila Monster bites on dogs reported in Tucson, Arizona, during 2001–02, two resulted in death of the Gila Monster (unpublished records, Arizona Poison Control Center). In most cases, each dog shook off the Gila Monster without seriously injuring it. From reviewing numerous case histories of *Heloderma* bites on humans (see below), I found only one instance in which the lizard was seriously injured while being extracted. In most cases, the lizard was forcefully pulled or pried off, and a few teeth broken, while attention was focused on the bite injury (and not on the lizard). It is plausible that, when bitten by a *Heloderma*, many natural predators would likewise extract the lizard without killing it. Occasionally, *Heloderma* may also be killed while being removed from an adversary. However, it seems unlikely that, if it survived being bitten, an adversary would eat the *Heloderma* (some of the bioactive peptides present in the venom may even suppress appetite; Szayna et al. 2000; Edwards et al. 2001). It is equally unlikely that an adversary would risk future encounters after a bite from one of these dangerous lizards (a fragment of the exendin peptide even helps improve memory; Haile et al. 2002). A predator, therefore, gains nothing by attacking a *Heloderma*, but it does risk injury, incapacitation, or death. Regardless of whether the *Heloderma* were killed, individuals bitten by Gila Monsters or Beaded Lizards would very likely show lower survivorship and reduced reproductive success. Over evolutionary time, predators learn to recognize and avoid noxious and potentially dangerous prey (S.M. Smith 1977; Lindstrom 2001). To the *Heloderma*, as long as the risk of death does not exceed the benefits received from reduced predation owing to recognition by predators, its defensive strategy would be successful. Because this genus has survived for at least 23 million years, it appears such a strategy has, indeed, been effective.

Whether or not the venom system seems efficient to us, *Heloderma* appears to have used it effectively for a long time. Natural selection does not produce adaptations that are perfect by any means, and half-baked solutions are often all that is possible given evolutionary constraints (Gould 1980). Natural selection is limited by the raw material it has to work with, in this case the morphological constraints imposed by the lizard body plan. Helodermatid lizards do not have agile, elongate bodies that enable them to coil and rapidly strike at a foe (that adaptive zone is the domain of the snakes), so a highly specialized venom apparatus designed for efficient injection of venom through hollow fangs does not make sense for *Heloderma*, given the niche it fills and the evolutionary constraints imposed by its generalized lizard morphology.

Lizards (including *Heloderma*) bite as a final means of defense, and when they do they tend to hang on. Interestingly, Alligator lizards of the genus *Elgaria* (family Anguidae, sister group to the Helodermatidae) bite in a manner similar to helodermatid lizards. Southern Alligator lizards (*Elgaria multicarinata*) readily bite when handled, hang on tenaciously when biting, and exert greater bite pressure (similar to the chewing actions shown by *Heloderma*) as attempts are made to extract them from a bitten extremity (personal observation). For a bite to be effective, a lizard may have no choice but to hang on. If the lizard releases its hold before an adversary has been effectively stunned, surprised, or immobilized (in the case of *Heloderma*), it would be vulnerable to subsequent capture and potential consumption. In this context, it makes sense why *Heloderma* behave as they do when they bite and why they do not possess a more "efficient" venom system. What helodermatids lack in their "crude" delivery system, however, they compensate for in a sophisticated array of venom constituents and bite tenacity. No doubt, the venom chemistry of *Heloderma* is efficient for defensive purposes.

One might more appropriately ask: Why are there not more lizards that use a venom system for defense? The answer might be that most lizards can run away more effectively than they can bite. However, there are rare cases where bites of varanid lizards may produce symptoms of toxicity (Ballard and Antonio 2001). In at least three cases, reptile keepers bitten by *Varanus griseus*, the Desert Monitor, showed symptoms ranging from dysphagia (difficulty swallowing), tightness of the chest muscles, and dyspnea (labored respiration) to dizziness, facial pain, and muscle soreness (Ballard and Antonio 2001). Desert monitor lizards have shown chewing motions during bites that may continue for over one minute. Whether these signs/symptoms are truly reactions to toxic peptides or proteins in the venom of *Varanus* needs to be thoroughly investigated.

Of the few other vertebrates known to use a venom system exclusively for defense, the Platypus *(Ornithorhynchus anatinus)* and Stonefish *(Synanceja horrida)* are noteworthy. Peptides and other components in Platypus venom relax smooth muscle in rats, promote edema and inflammation, and produce extreme pain (Fenner et al. 1992; De Plater et al. 1998). Stonefish venom produces intense pain and induces hypotension via relaxing smooth muscle in the walls of blood vessels (Low et al. 1993). These venoms act to repel and potentially immobilize potential predators with symptoms (severe pain, inflammation, and hypotension) similar to those produced by bites of *Heloderma*. Spitting cobras seem to have evolved the ultimate venom delivery system for defense. Venom is ejected from the fangs as a jet that becomes a fine spray (Bogert 1993). A tiny speck of African Spitting Cobra, *Naja nigricollis*, venom landing in the eye produces a pain, in the words of a photographer affected by the venom, greater than any ever experienced (Bogert 1993).

In contemporary helodermatid lizards, the venom system functions as an effective defense mechanism, while some of the bioactive peptides in the venom could play a role in digestion. The venom proteins and peptides appear to act primarily on initiating a powerful inflammatory/pain response, relaxing smooth muscle (which results in vasodilation and hypotension), and influencing energy metabolism. Taken together, the venom constituents clearly act physiologically to immobilize or incapacitate the bite victim. Some of these components not only profoundly affect the physiology of potential mammalian adversaries, but they are, in a sense, *part* of their physiology. These venom components are analogues of important mammalian hormones, including serotonin, secretin, VIP, and GLP-1. The kallikrein enzymes are common participants in the inflammatory response in mammals. As noted above, many of the bioactive peptides (helospectin and helodermin, in particular) have been located, using immunohistochemical techniques, in several mammalian tissues including the brain, pancreas, blood, colon, lung, stomach, breast, heart, intestine, uterus, liver, urogenital system, and others (Raufman 1996). In these tissues, they appear in association with membrane receptors that play a role in regulating secretory activities and local blood flow. When they were first discovered, it was thought that some of the bioactive peptides in *Heloderma* venom represented homologues of mammalian hormones yet to be discovered (Parker et al. 1984). This appears not to be the case; for example, helodermin and exendin-4 from *Heloderma* are not the evolutionary precursors to mammalian VIP and GLP-1. They are distinct peptides encoded by different genes and, therefore, appear to have evolved independently of the mammalian peptides they resemble (Chen and Drucker 1997; Pohl and Wank 1998). To find so many *Heloderma* venom peptide sequences within the tissues of mammals suggests an intricate example of biochemical mimicry. The venomous bite of helodermatid lizards has apparently evolved to incapacitate and deter an enemy with a diversity of toxins that manipulate its physiology in a variety of ways. An intriguing possibility also exists that exendin, and perhaps other bioactive peptides in the venom of Gila Monsters and Beaded Lizards, may act to regulate the lizards' own digestive physiology (Young et al. 1999b). What has previously been called a "primitive," "crude," or "inefficient" venom system appears, in fact, highly refined and effective.

Since the early 1980s, when many of the constituents of *Heloderma* venom were discovered, little attention has been directed at whole-venom physiological effects. When taken as a whole, many of the venom components may show synergistic consequences that are not apparent when examined alone. For example, gilatoxin shows greater toxicity when combined with other venom components than when acting alone (Tu 1991). It is likely that other venom constituents, especially the kinin-releasing peptides and the bioactive peptides, may interact in similar ways. Investigations into how the venom components may interact with one another in mammalian tissues would be another fruitful arena for future research (chap. 10). A picture of whole-venom effects partially emerges by examining the effects of *Heloderma* envenomation in humans, which we consider next.

HUMAN ENVENOMATION BY *HELODERMA*: OVERVIEW OF BITE CASE HISTORIES

A rich, entertaining, and commonly erroneous literature is associated with bite case histories of *Heloderma* (see chap. 1). Vivid tales abound recounting suffering, terror, and death. I have found more exaggerated and erroneous information associated with this *Heloderma* topic than with all others combined. Woodson (1947) provided one of the first summaries of the bite of *Heloderma*, reporting that 29 of 136 cases ended in death. Bogert and Martín del Campo (1956) summarized 34 cases between the 1880s and 1956, mostly from newspaper clippings and correspondence, eight of which allegedly resulted in death. Both Woodson (1947) and Bogert and Martín del Campo (1956) emphasized that details regarding deaths from *Heloderma* bites were often sketchy, contradictory, and invalidated, and that alcohol was involved in most cases. Russell and Bogert (1981) discussed the outcomes of another 16 cases, as well other published records available to them (Shannon 1953; Bogert and Martín del Campo 1956; Grant and Henderson 1957; Albritton et al. 1970; Stahnke et al. 1970). None of the 16 cases mentioned by Russell and Bogert resulted in death. Since the dubious case in 1930 of an intoxicated pool-hall operator in Casa Grande, Arizona (chap. 1), there have been no authenticated reports of a death from the bite of *Heloderma suspectum*. In fact, I have not even been able to find any published validated cases of truly "legitimate" bites (i.e., victims being accidentally bitten by wild Gila Monsters that were not poked, picked up, handled, or otherwise harassed).

Hearsay and fertile imaginations have, therefore, produced far more information about the bite of *Heloderma* than have scientific records and reports. Of the many bite cases reported in newspapers, correspondences, and the popular literature since 1950, I could find only 17 that were based on firsthand information and published in peer-reviewed biological or medical journals (tables 7 and 8). Even in these cases, one description of a myocardial infarction following the bite of a Gila Monster (case no. 11, tables 7 and 8) was published twice, by different authors in 1988 and 1989 (Bou-Abboud and Kardassakis 1988; Preston 1989). A summary of these bites and their signs and symptoms are given in tables 7 and 8. Since 1950, bites by *Heloderma* have become less newsworthy, so only the most serious or noteworthy cases get reported in scientific journals. Since 1981, I could find only 10 such cases. Tables 7 and 8 do not include cases reported in the news media (unless they are also published in a peer-reviewed journal), or those contained in unpublished hospital records, regional reports, etc. Tables 7 and 8 should be interpreted carefully, therefore, because, although they contain some of the best-documented cases, they are not necessarily the most representative.

TABLE 7

Heloderma *Bite Cases Published in Peer-Reviewed Journals since 1950*

CASE NO.	CAUSE (ALL FROM CARELESS HANDLING)	BITE LOCATION	REFERENCES
1	Pet	Finger	Shannon 1953
2	Pet	Finger	Shannon 1953
3	Demonstration	Finger	Tinkham 1956
4	Demonstration	Thumb	Grant and Henderson 1957
5	Demonstration	Finger	Albritton et al. 1970
6	Demonstration	Finger	Stahnke et al. 1970
7	Pet	Hand	Roller 1977
8	Pet	Abdomen	Heitschel 1986
9	Wild capture	Forearm	Piacentine et al. 1986
10	Pet	Hand	Streiffer 1986
11	Wild capture	Forearm	Bou-Abboud and Kardassakis 1988 and Preston 1989
12	Recent capture	Calf	Caravati and Hartsell 1994
13	Wild capture?	Thumb	Caravati and Hartsell 1994
14	Pet	Shoulder	Caravati and Hartsell 1994
15	Wild capture	Triceps	Caravati and Hartsell 1994
16	Pet	Finger	Strimple et al. 1997
17	Pet	Hand	Cantrell 2003

Nevertheless, an analysis of the cases summarized in tables 7 and 8 is instructive. Most bites were to a finger or hand and came from pet Gila Monsters. These bites are more likely to produce intense pain and local edema but are less likely to produce more serious symptoms such as severe hypotension, cardiac and blood abnormalities, or shock. All bites resulted from careless handling, some of which occurred during public demonstrations or classroom lectures. Alcohol was involved in some of the most serious cases (Heitschel 1986; Piacentine et al. 1986; Caravati and Hartsell 1994).

Based on an examination of case histories by Bogert and Martín del Campo (1956), Russell and Bogert (1981), recent bite case reports (tables 7 and 8), and my knowledge of approximately 30 unreported or untreated bites over recent years, the most common signs and symptoms of *Heloderma* envenomation in humans are similar to those observed in other mammals (table 4). They include pain, local edema, and a feeling of weakness, faintness, or nausea. Bleeding at the site of the bite may be profuse, not from anticoagulant effects of the venom, but from the lacerating effect of the teeth and tenacity of the bite (fig. 13). Pain, often severe, usually begins within minutes, and may last several hours. The pain has been described as a steady burning, like a spine imbedded in the flesh. Pain may spread well beyond the site of the bite; a person bitten on the arm may feel pain from the shoulder to the hand. Edema (swelling) can occur within minutes and extend well beyond the region of the bite (fig. 13).

A second set of relatively common symptoms includes hypotension, sweating, an increased heart rate, and vomiting. Blood chemistry changes, including elevated leukocyte count, reduced potassium levels, and reduced platelets, are occasionally shown in moderately severe cases (tables 7 and 8). There is limited evidence that previous exposure to *Heloderma* bites may sensitize some individuals and result in an allergic reaction to the venom (Cantrell 2003). More severe cases seem to result from bites located closer to the core of the victim's body, such as the abdomen, shoulder, calf, or forearm (tables 7 and 8). The most severe cases result in extreme hypotension, which may be accompanied by life-threatening anaphylaxis (Piacentine et al. 1986), coagulopathy and acute myocardial infarction (Bou-Abboud and Kardassakis 1988), or profuse diarrhea and lethargy (Heitschel 1986). These cases likely illustrate the powerful physiological effects of the kallikrein-like and bioactive peptides found in *Heloderma* venom.

TABLE 8

Bite Signs/Symptoms and Their Frequency

	PERCENT (%) OF CASES	CASES REPORTING (FROM TABLE 7)
Pain	82	1–3, 5–8, 10–13, 15–17
Local edema/swelling	82	1–7, 9–11, 13, 15–17
Weakness, faintness, dizziness	65	1, 3, 4, 6, 8, 11–13, 15–17
Nausea	65	2, 3, 5–8, 10, 12, 14, 16–17
Hypotension	47	6, 8–14
Diaphoresis (sweating)	47	4, 8–11, 13, 16–17
Tachycardia (elevated heart rate)	35	5, 8, 11, 12, 14, 15
Vomiting	35	3, 5, 10, 12, 14, 17
Leucocytosis (elevated WBC count)	29	6, 8, 11, 12, 17
Hypesthesia (hypersensitivity around bite)	24	1, 2, 12, 16
Reduced blood potassium levels	18	8, 9, 11
Reduced platelets	18	8, 11, 17
Cyanosis (bluish discoloration around bite)	13	3, 8
Cardiac abnormalities	12	7, 11
Swollen or painful lymph glands	12	10, 11
Lethargy	12	8, 14
Anaphylaxis	6–12	9, possibly 17
Diarrhea	6	8
Tinnitis (ringing in ears)	6	2
Exophthalmia or periorbital hemorrhage	6	8
Hypothermia	6	12
Miosis (contraction of pupil)	6	14

In the most serious case, a young woman had hidden a Gila Monster under her sweater and walked into a tavern, whereupon the lizard bit her on the abdomen. Her screams alerted bar patrons of her condition, and her boyfriend removed the lizard by severing its head. When she arrived at the hospital, the woman was nearly incapacitated, showing severe pain, vomiting, and diarrhea. She remained in intensive care for 36 hours (Heitschel 1986). This case (the only female in the sample) is noteworthy because the victim's symptoms are similar to pancreatic cholera, a condition produced by VIP-secreting tumors and also known as WDHA (watery diarrhea, hypokalemia, acidosis) syndrome (Connigrave and Young 1996). Such symptoms may be an example of the action of VIP-like bioactive peptides in *Heloderma* venom.

TREATMENT OF BITES

Bites by *Heloderma* may be increasing because, as captive-breeding techniques have improved, more people are keeping these lizards in private collections (chap. 8). The docile nature of *Heloderma* kept in captivity often lulls their handlers into a dangerous habit of complacency. The vast majority of bites by helodermatid lizards occur on the fingers or hands.

FIGURE 13. Bite to the index finger from a *Heloderma suspectum*. The laceration occurred as the Gila Monster was extracted from the finger. Considerable edema that commonly occurs from Gila Monster bites had already subsided when this photograph was taken two days later (photo by M.L. Gilbert).

Most of these pass on uneventfully and go unreported (Miller 1995). Although a *Heloderma* bite is very unlikely to be lethal to a healthy adult, it should nevertheless be considered a serious medical emergency. A common misconception is that only the dentaries in the lower jaw (and to a lesser extent the maxillaries in the upper jaw) can deliver sufficient venom to cause serious effects. This is not the case; significant symptoms can occur by a seemingly minor "slashing" bite from even the premaxillary teeth toward the front of the mouth (Tinkham 1956; Strimple et al. 1997).

When a person is bitten by a *Heloderma*, the following first aid measures are recommended:

1. Remove the lizard as quickly as possible. The longer the lizard bites, the more venom it is able to deposit into the wound and the more likely the bite is to produce serious symptoms. In mild bites, where only a fold of skin is bitten, it may be possible to simply hold the lizard behind the jaws and carefully pull it away; in cases where the jaws are more firmly attached, it may be necessary to pour water on the lizard or to pry it off with pliers or some other device. A thin, flat lever inserted between the lower jaw and the flesh and turned 90 degrees may work to quickly release the jaws. When *Heloderma* are forcefully removed from the bite site, as is often required, teeth are usually pulled out and a laceration results (fig. 13). I do not recommend trying to remove the lizard by applying a flame to its chin or by using dangerous solvents such as gasoline (which have been advocated in the past). These measures only add to the possibility that additional injury and pain will result.
2. Immediately remove any rings, bracelets, or other jewelry (including piercings). These articles may cause complications as edema (swelling) develops.
3. The bitten part should be immobilized; a light cloth bandage and mild pressure may be applied to control any bleeding.
4. The victim should be transported (by another person) to medical care as quickly as possible and reassured that they will not die.
5. DO NOT apply stun guns, heat, or ice to the wound. DO NOT use tourniquets or constriction bands of any kind nor make incisions to suck out venom.

Once the victim has arrived at the hospital, vital signs should be monitored immediately. One of the biggest dangers is shock/hypotensive crisis brought about by a rapid fall in blood pressure. This can be treated in the victim by infusing electrolyte solutions and administering antishock drugs. Pain normally peaks within 1 to 2 hours, but may linger for days (Caravati and Hartsell 1994). It can be difficult to relieve; analgesics and morphine have been used effectively (Strimple et al. 1997). Edema normally peaks within 2 to 4 hours and resolves itself without special measures within 72 hours. Because it is largely subcutaneous, edema has not been reported to cause compartment syndrome or neurological problems. Depending on the severity of the bite, laboratory blood tests should be performed to assess the possibility of electrolyte imbalance, leukocytosis, and coagulopathy, which have been reported previously (see tables 7 and 8). An electrocardiograph should be used to evaluate any heart anomalies; myocardial conduction disturbance (Roller 1977) and myocardial infarction (Bou-Abboud and Kardassakis 1988) have been observed. Antihistamines or corticosteroids are usually unnecessary because allergic reactions are rare, although one case of anaphylaxis has been reported (Piacentine et al. 1986). The wound should be carefully inspected for any broken teeth and thoroughly cleaned with antiseptic. Soft-tissue radiography is not sufficient to locate broken teeth (Caravati and Hartsell 1994). Antibiotics are routinely given, although tissue necrosis and infections are very rare. Tetanus immunization should be updated if necessary. Most victims of *Heloderma* envenomation are released from the hospital within 24 hours and recover completely within 2 weeks. More severe cases may require hospitalization up to 48 hours (e.g., Heitschel 1986).

CHAPTER 4

Physiological Ecology

IN JULY 2002, TAKERU Kobayashi broke the world hot dog–eating record by engulfing 50.5 franks in 12 minutes. Kobayashi weighed 113 lb at the start of the contest and 129 lb at the end, having eaten 16 lb of food, equivalent to 14% of his body mass. This is an exceptional feat for a human. In the summer of 1983, I watched a 640-g Gila Monster devour four newborn cottontail rabbits, together weighing 210 g, equivalent to 33% of its body mass. Although this was an important energetic event for the Gila Monster, it was no exceptional accomplishment for a squamate reptile. Some venomous snakes, for example, are capable of consuming prey exceeding 125% of their body mass (Greene 1997).

A typical hot dog contains about 160 calories (each calorie is equal to 1 kilocalorie [kcal], or 4.184 joules, the standard unit for expressing energy content). Thus Kobayashi's big meal contained just over 8,000 kcal, which is about four times the standard 2,000 calorie/day diet for an average person. Kobayashi's meal might, therefore, sustain him for about 4 days. The Gila Monster's meal, on the other hand, would sustain it for nearly 4 months (see below). The energy efficiency of the lizard becomes even more impressive when we consider differences in size. Kobayashi weighed about 80 times as much as the Gila Monster. Smaller animals generally use less energy than larger ones, but, on a per gram basis, smaller animals actually have higher metabolic rates. In vertebrates, a 50% reduction in mass results in a decrease in *mass-specific* metabolic rate of only about 34% (McNab 2002). So if we scaled Kobayashi down to the size of our 640-g Gila Monster, his metabolic rate would be proportionately much greater—and a meal equivalent to 14% of his body mass would sustain him for barely 24 hours. A meal comprising 14% of the body mass of the Gila Monster, on the other hand, could sustain the lizard for nearly 8 weeks (see below). And if we scaled the Gila Monster up to the size of Kobayashi (and assumed its mass-specific metabolic rate decreased proportionately), a meal of 50 hot dogs would sustain the lizard for well over a year!

The striking difference in energy use between a human and a Gila Monster illustrates the amazing energy efficiency of ectothermic, or *cold-blooded*, vertebrates. As ectotherms, helodermatid lizards rely on external sources of heat to regulate body temperature. For an ectotherm, the heat produced through metabolism contributes little to maintaining a body temperature suitable for foraging activity, digestion, etc. Endotherms, on the other hand, release considerable heat from energy metabolism, which, in turn, allows them to maintain relatively high and constant body temperatures, even when the surroundings are relatively cold. Endotherms are thus free to remain active (and eat hot dogs) even when environmental conditions are too cold for most ectotherms.

But this freedom comes at an energetic cost (Pough 1980). A free-living bird or rodent, for example, expends 20 to 40 times as much energy per day as a comparable reptile (Nagy 1982). Ectotherms have thus been described as "low-energy systems" (Pough 1983), a trait which gives them an advantage in low-productivity environments such as deserts. Even for an ectotherm, however, helodermatid lizards are among the most frugal energy consumers (Beck and Lowe 1994). In this chapter, I'll use thermal biology and ecological energetics as a backdrop for discussing the unique physiological ecology of helodermatid lizards and the ability it affords them to thrive in variable environments.

THERMAL BIOLOGY

Physiological processes function best within a range of temperatures referred to as the thermal-performance breadth (see Huey and Stevenson 1979; Huey 1982). In the best of worlds, body temperature might be regulated within this range in a way that maximizes the numerous underlying physiological processes that are affected by temperature. For ectotherms, however, constraints in nature (both physical and biological) limit just how effectively body temperature can be regulated (C. R. Peterson 1987). Warm temperatures that are optimal for activity may not occur on cool, cloudy days. Basking on a warm rock allows a lizard to regulate its body temperature, but also increases its exposure to predators. Thermal preferences can also change with age, season, and physiological condition (Beuchat 1986; Lillywhite 1987; C. R. Peterson et al. 1993; Beck 1996). Gravid lizards may behaviorally maintain higher body temperatures (Stewart 1984), and many reptiles show a thermophilic response after feeding (Regal 1966; Huey 1982; Beck 1996). The thermal biology of helodermatid lizards, therefore, represents the simultaneous coordination of many factors that affect body temperature. Optimal temperatures may be impossible to achieve at all times, but body temperature must never exceed the limits of physiological tolerance.

THERMAL TOLERANCE

Helodermatid lizards do not tolerate high body temperatures. During normal foraging activity, they usually avoid body temperatures above 35°C by seeking cooler microenvironments in the shade of shrubs, trees, or boulders. Occasionally, thermal inertia will carry body temperature (T_b) over 37°C, but I have never recorded a Gila Monster or Beaded Lizard voluntarily active at a body temperature above 37°C (figs. 14 and 15). This temperature, however, may be well below the critical thermal maximum. The critical thermal maximum is the upper body temperature at which an animal either can no longer right itself if turned over or exhibits uncontrolled muscular spasms (Lutterschmidt and Hutchison 1997). Although it is not physiologically lethal, the critical thermal maximum may be ecologically lethal because it prevents the lizard from taking voluntary action to keep its body temperature from increasing to truly lethal levels (Pough and Gans 1982). Bogert and Martín del Campo (1956) exposed a Gila Monster to the hot sun and the lizard became partially paralyzed at a T_b of 42.5°C and completely paralyzed at 44.2°C, although it eventually recovered. This result suggests that the critical thermal maximum for *Heloderma* is around 44°C and that helodermatid lizards are thermally conservative during activity in nature, avoiding body temperatures within at least 7°C of their critical thermal maximum. Such a conservative thermoregulatory strategy makes sense given their relatively large body size and the consequent potential for thermal inertia to send them over a dangerous temperature threshold. Avoidance of high body temperatures may also help lizards

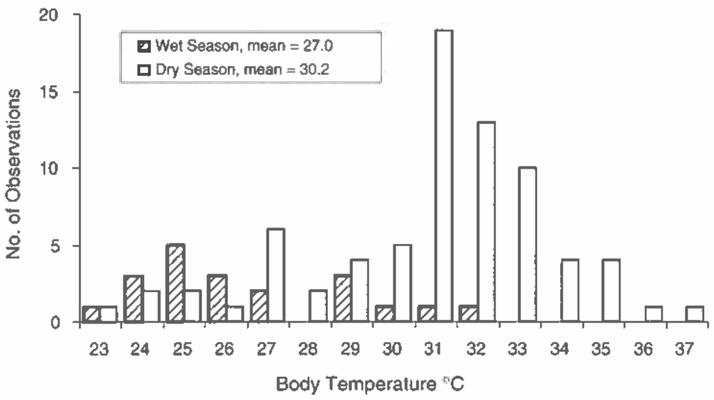


FIGURE 14. Body temperatures of surface-active *H. horridum* in Jalisco, Mexico (after Beck and Lowe 1991). Activity temperatures tend to be lower during the wet season (July–October), when activity frequently occurs during rainy periods.

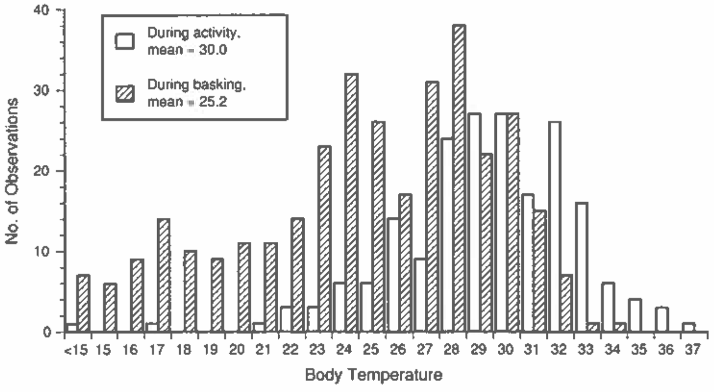


FIGURE 15. Body temperatures of *H. suspectum* recorded during activity in comparison with those during basking in Arizona, New Mexico, and Utah (unpublished data from D. Beck, B. Martin, and C. Lowe). Cooler temperatures represent those measured from lizards shortly after they have emerged from shelters.

reduce rates of evaporative water loss and escape dehydration.

Gila Monsters appear to be more tolerant of cold temperatures than of heat. Late on a cool April day, I recorded body temperatures of 17°C near the end of a lengthy fight between two males (air temperature was below 10°C). Temperatures throughout the range of *H. suspectum* commonly drop well below freezing in winter. Gila Monsters occasionally experience body temperatures below 10°C during winter dormancy (see below), and they apparently tolerate temperatures much colder. At prolonged exposure to body temperatures as low as 4.6°C, Gila Monsters retain the abilities of hissing by forcefully exhaling and righting themselves when turned on their backs (Bogert and Martín del Campo 1956). Gila Monsters lose the ability to crawl when their body temperatures drop below 10°C; the tongue can no longer be thrust out at body temperatures below 8°C (Bogert and Martín del Campo 1956). Gila Monsters can likely survive temperatures below freezing; their supercooling limit is −3.89°C (Lowe et al. 1971). *Heloderma horridum* is probably much less tolerant of cold than is *H. suspectum*. Body temperatures of Beaded Lizards rarely drop below 15°C in nature; the coldest body temperatures I have recorded from Beaded Lizards were 17.7°C in January. At my study site in Jalisco, Mexico, air temperatures rarely drop below 8°C. Freezing temperatures are largely nonexistent in tropical dry forest habitats of *H. horridum* (see chap. 5).

TABLE 9

Mean Activity Temperatures of Helodermatid Lizards Measured in Nature

	SPECIES	REFERENCE
29.3°C	*suspectum*	Coombs 1977
29.3°C	*suspectum*	Porzer 1981
29.4°C	*suspectum*	Beck 1990
29.0°C	*suspectum*	Lowe et al. 1986
30.1°C	*suspectum*	B. E. Martin and Lowe unpublished
30.0°C	*suspectum*	Beck 1994
31.0°C	*suspectum*	Gienger 2003
26.7°C (August) 25.2°C (September)	*suspectum*	[a]DeNardo et al.
30.2°C (dry season) 27.2°C (wet season)	*horridum*	Beck and Lowe 1991

[a]Primarily nocturnal activity, determined from temperature-sensing iButton dataloggers.

ACTIVITY TEMPERATURES

The body temperatures at which a free-ranging reptile engages in its normal activity routine constitute its "activity temperature range" (Pough and Gans 1982). The "mean activity temperature" is the mean of the body temperatures within that activity temperature range (Pough and Gans 1982). In nature, *H. horridum* shows a mean activity temperature of 29.5°C and an activity temperature range of 22.5°C –36.0°C (Beck and Lowe 1991). Interestingly, *H. horridum* shows a slightly higher mean activity temperature during the dry season (30.2°C) than during the wet season (27.0°C), when lizards commonly emerge from shelters and walk in the rain (fig. 14).

In nature Gila Monsters show a mean activity temperature similar to that of *H. horridum*. A number of field studies on *H. suspectum* indicate that their mean activity temperature is very near 30.0°C (table 9), regardless of geographic location. The activity temperature range is from 17.4°C to 36.8°C, although activity rarely occurs at body temperatures below 24°C (Beck 1990; fig. 15). These field activity temperatures are in close agreement with estimates from the laboratory. Bogert and Martín del Campo (1956) measured body temperatures of three *H. suspectum* active in a laboratory thermal gradient. Body temperatures ranged from 24.3°C to 33.7°C with the mode falling between 29°C and 30°C (Bogert and Martín del Campo 1956).

In comparison with other lizards, the activity temperatures of helodermatids are relatively low. Mean activity temperatures range from 21°C in alligator lizards *(Elgaria)* to over 40°C in some desert species such as the Desert Iguana *(Dipsosaurus dorsalis)* and whiptail lizards (*Cnemidophorus sp*; Brattstrom 1965; Avery 1982). Some desert lizards, including *Callisaurus draconoides* (Zebra-tailed Lizard), *Dipsosaurus dorsalis* (Desert Iguana), and *Uma notata* (Fringe-toed Lizard) frequently tolerate body temperatures that are near their upper physiological limits, and certainly well beyond that for *Heloderma* (Dawson 1975).

What are the consequences of a relatively low activity temperature? Because the potential for evaporative water loss increases greatly at higher body temperatures (Mautz 1982), and because *Heloderma* has relatively high rates of evaporative water loss when compared with other lizards (Lowe et al. 1986; DeNardo et al. 2004; see below), a lower activity temperature

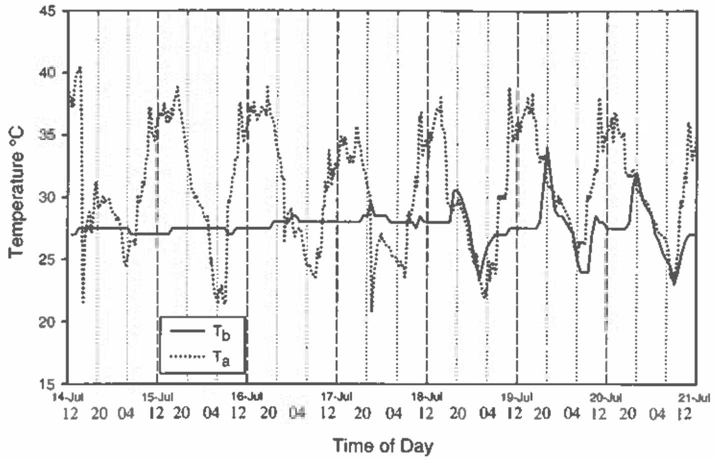


FIGURE 16. Body temperatures of a Gila Monster (T_b) outfitted with an iButton miniature temperature-sensing datalogger plotted in relation to concurrent air temperatures (T_a). Body temperature is stable when the lizard remains within shelters but fluctuates considerably during above-ground forays. Vertical grid lines represent 8-hour intervals (after DeNardo et al. unpublished data).

may reduce rates of evaporative water loss during activity. Water loss rates may be three to four times higher in active than in quiescent animals (Mautz 1982). A low activity temperature also permits *Heloderma* to be active at night, when options for maintaining higher activity temperatures are not available.

Before the mid-1940s, it was generally believed that ectotherms were restricted to accepting body temperatures that were largely the same as their surroundings. The discovery that ectotherms can achieve thermal homeostasis by behavioral adjustments (e.g., Cowles and Bogert 1944) revolutionized our understanding of vertebrate body temperature regulation. Some lizards are able to regulate body temperature within a fairly narrow range (<2°C) during activity (e.g., Cowles and Bogert 1944; DeWitt 1967). How precisely do *Heloderma* regulate their body temperature? The activity temperatures shown in figures 14 and 15 suggest that helodermatid lizards actually accept a relatively wide range of body temperatures during activity, allowing body temperatures to vary from around 24°C to 34°C. Using implantable, temperature-sensing dataloggers, DeNardo and his students found that *H. suspectum* allow their body temperature to vary considerably when they are surface-active, ranging from approximately 23°C to 34°C (fig. 16). Although thermoregulatory precision has yet to be carefully tested in helodermatid lizards, they do not appear to regulate body temperature within narrow limits when they are active. Another perspective on behavioral thermoregulation by *Heloderma* can be gained by examining body temperatures during basking.

BASKING BEHAVIOR

In Arizona and New Mexico, sun basking most commonly occurs at the entrance to shelters during February through May. In Utah, the basking period is more restricted, primarily to late March through May (and less commonly on cool summer days). In Arizona, Gila Monsters may be found basking during any month of the year, although basking is much rarer during summer months and occurs at this time only on cool, overcast days or after rain. Body temperatures during basking tend to be cooler than activity temperatures (fig. 15), primarily because the purpose of basking is to behaviorally increase body temperature. During basking, Gila Monsters may occasionally regulate body temperature within fairly narrow limits.

Figure 17 summarizes the thermal patterns shown by a Gila Monster basking at its shelter entrance during a typical session in April. The Gila Monster exits its shelter in the morning about an hour after sun strikes its east-facing entrance. It flattens its body while orienting its long axis toward the rays of the morning sun (fig. 17). Within a few minutes, the Gila Monster's body temperature begins to rise. As its body temperature approaches 30°C, the lizard begins to shuttle into and out of its shelter, maintaining its body temperature between 28°C and 31°C throughout the morning. During mid-afternoon, as surface temperatures exceed 35°C, the Gila Monster moves back into its shelter, then reemerges briefly before retreating inside its shelter until the next morning.

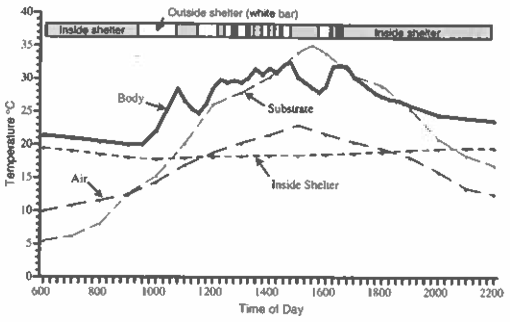


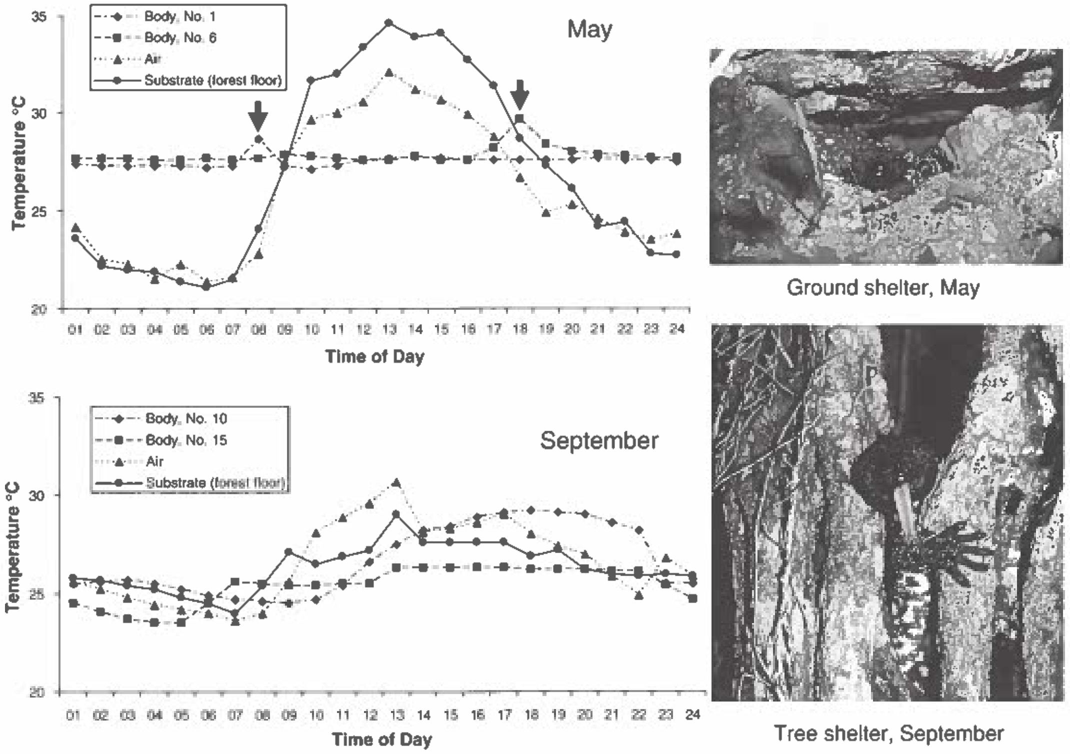
FIGURE 17. In early spring, Gila Monsters occasionally bask near shelter entrances on "aprons," which may face the morning sun. The graph details thermal relationships of a Gila Monster throughout an April day in southwestern Utah. White areas within the bar at top indicate periods when the lizard is basking in the sun; shaded areas show periods when the lizard moves back inside its shelter. The photograph shows the Gila Monster during a basking period on the same day.

During such basking sessions, Gila Monsters show active thermoregulatory behaviors (moving in and out of shelter; flattening body against substrate, positioning long axis of body toward the sun's rays), and they seem to regulate body temperature within a relatively narrow range (between 29°C and 32°C; fig. 17). At times only a portion of the body may be extended outside of the shelter and exposed to the sun. Interestingly, on many days where extended basking occurs, lizards do not move away from their shelters and actively forage but instead merely shuttle into and out of the shelter throughout the basking period. Some of these basking sessions may serve to rekindle various physiological processes that have remained dormant for the extended periods spent at low body temperature during winter months. Spring basking can also be associated with such reproductive behaviors as male combat and pairing of individuals within shelters (Beck 1990; chap. 8).

Heloderma horridum also occasionally bask. In Chamela, I've observed Beaded Lizards sun basking during January and after summer rains. One lizard, monitored while sun basking in a tree after a heavy September rain, maintained its body temperature between 28.2°C and 29.4°C (mean = 28.8°C) between the hours of 1415 and 1620. Air temperature during this period fell from 28.4°C to 26.8°C (Beck and Lowe 1991).

BODY TEMPERATURES WHEN AT REST

Although *Heloderma* commonly bask at shelter entrances, and occasionally appear to regulate body temperature within a specific range, they spend the majority of their time as thermoconformers, passively accepting the temperature of their shelter environment. This is illustrated in figure 16, which shows that while Gila Monsters



Ground shelter, May

Tree shelter, September

FIGURE 18. Thermal relationships of *H. horridum* in a tropical dry forest in Jalisco, Mexico (after Beck and Lowe 1991). Body temperatures remain relatively constant when lizards are in ground shelters (May), despite strong fluctuations in air and substrate temperatures. Abrupt changes in body temperatures (arrows) coincide with brief periods of surface activity. Body temperatures may be more variable during the wet season (September) when Beaded Lizards, shown here, are using shelters in trees (which are less buffered from swings in environmental temperatures), even though air and substrate temperatures are less variable than during the dry season.

are resting in belowground shelters body temperatures typically fluctuate very little over the course of a 24-hour period.

In Chamela, Jalisco, Mexico, body temperatures of Beaded Lizards at such times are highly correlated with the temperature at 0.5 m below ground (near the depth Beaded Lizards are positioned within shelters), but they are not correlated with surface or air temperatures (Beck and Lowe 1991). When a lizard moves to a new shelter, body temperature changes depend on the thermal characteristics of the new shelter. For example, Beaded Lizards using shelters in trees, which are less buffered from daily temperature swings than are ground shelters, show considerable fluctuation in body temperature over 24 hours (fig. 18). Lizards in tree shelters have body temperatures more highly correlated with air temperatures than with the temperature at 0.5 m below ground (Beck and Lowe 1991). The general pattern, however, is for *Heloderma* body temperatures to remain strikingly constant as long as they remain inside shelters, which may be for over 95% of the time (chap. 5).

Given that helodermatid lizards inhabit seasonal environments, it stands to reason that body temperatures should show significant seasonal fluctuations, and these changes would be greater in the more thermally variable environments inhabited by Gila Monsters than in the more thermally stable tropical dry forest habitats of *H. horridum*. Figure 19 compares the mean monthly body temperatures of *H. horridum* resting within shelters in Chamela, Jalisco, with those of *H. suspectum* in Redrock, New Mexico, approximately 2,000 km to the north. Mean monthly body temperatures of the Jalisco Beaded Lizards ranged from 19.9°C in December to 28.5°C in July (fig. 19). Extreme body temperatures ranged from 17.7°C in January to 37.2°C (thermal inertia after activity) in June. Not surprisingly, the New Mexico Gila Monsters have cooler body temperatures; monthly means range from 27.6°C in July to 12.8°C in January (fig. 19). Extremes in body temperatures of Gila Monsters in shelters range from 9.1°C (in December) to 36.8°C (thermal inertia after activity in June). Body temperatures usually fairly closely track ambient temperatures measured within shelters (fig. 20). Because temperatures vary among different shelter types (e.g., rocky shelters tend to be warmer than soil burrows), body temperatures of lizards may vary with shelter type (Beck and Jennings 2003; chap. 5). Still farther north, in Utah, mean body temperatures do not appear appreciably different from those of the New Mexico Gila Monsters (Beck 1990).

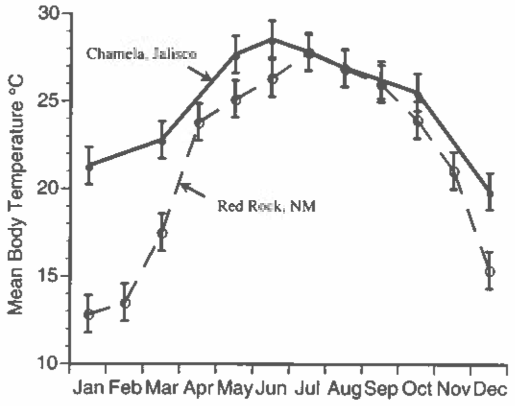


FIGURE 19. Comparison of mean monthly body temperatures of *H. horridum* from Jalisco, Mexico, with *H. suspectum* from New Mexico, USA, 2,000 km to the north (± 1 SD [horizontal lines]). Data from D. Beck and C. Lowe (1991 and unpublished), Beck and Jennings 2003, and D. Beck (unpublished).

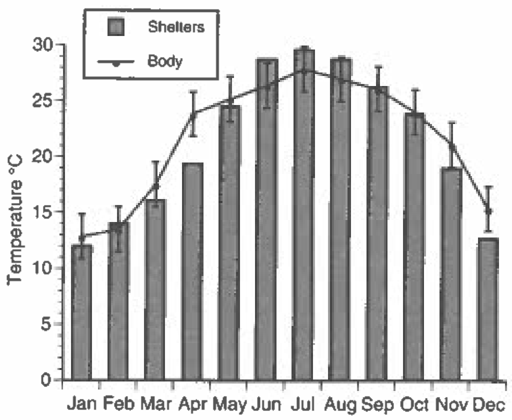


FIGURE 20. Mean monthly body temperatures of *H. suspectum* resting in shelters in southwestern New Mexico. Each shelter temperature shown is the monthly mean of nine different kinds of shelters (rocky crevices, burrows, etc.) occupied by Gila Monsters on the study site. Body temperatures fairly closely track shelter temperatures throughout the year. Differences between body and shelter temperatures occur during seasons when lizards are basking (e.g., March–April) or have selected specific shelters that are warmer (e.g., winter) or cooler (e.g., summer) than the norm. Data from D. Beck and R. Jennings 2003 and unpublished.

These seasonal patterns of body temperature variation in helodermatid lizards show that a good deal of the year is spent at body temperatures below 25°C (for *H. horridum*) or 20°C (for *H. suspectum*). These relatively low temperatures may have important implications for energy conservation in helodermatid lizards because metabolic rates are greatly reduced at lower temperatures. Just how substantial are these energy savings? To answer this, we must first consider the metabolic rates of helodermatid lizards.

ENERGETICS

Because all organisms demand energy and because it is often scarce and difficult to obtain, the role of energy acquisition and use plays a central role in physiological ecology (see McNab 2002). The rate at which an animal uses energy (its metabolic rate) can be readily determined by measuring its rate of oxygen consumption in the laboratory. Metabolic rate obviously varies depending on whether an animal is sleeping, alert, or active. For ectotherms, the term *standard metabolic rate* (SMR) is used for measurements of oxygen consumption, and hence metabolic rate, from inactive, postabsorptive individuals during the time of day when they are normally inactive (Andrews and Pough 1985). Measurements of oxygen consumption from postabsorptive lizards that are resting, but remain awake and alert, are referred to as *resting*

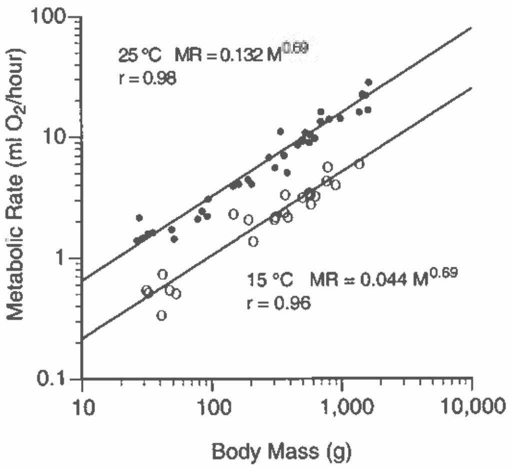


FIGURE 21. Relationship between body size (mass) and metabolic rate in helodermatid lizards (after Beck and Lowe 1994). Gila Monsters and Beaded Lizards have nearly identical metabolic rates so the data have been pooled from both species to provide the combined equation shown here. With a decrease of 10°C, metabolic rate decreases threefold (i.e., $Q_{10} = 3$).

metabolism. Defining metabolic rate in this way allows researchers to make fair comparisons of metabolic rates among various groups.

METABOLIC RATES

Early researchers discovered that although larger animals have higher metabolic rates than smaller ones, on a mass-specific basis, metabolic rate actually decreases as body size increases (e.g., Kleiber 1947, 1961). If metabolic rate is plotted as a function of body mass on a graph, metabolic rate increases with body mass to the 0.70 to 0.80 power (McNab 2002). The power to which metabolic rate is raised (equal to the slope of a regression line when the relationship is expressed on a graph with log–log axes) is termed the *mass exponent* (see fig. 21). The mass exponent is important because it describes the nature of the relationship between body mass and energy use. Thus, a mass exponent of 0.75 leads to an increase in metabolic rate of 75% with a doubling in body mass (or, put another way, a doubling of body mass leads to a 25% *decrease* in *mass-specific* metabolic rate). In an analysis of 107 species of lizards and snakes, Andrews and Pough (1985) derived a very useful equation describing the relationship between body mass and metabolic rate. For their comparison of adults of many species of lizards and snakes, they obtained a mass exponent of 0.80. Their equation serves as a standard to which other lizard groups, including *Heloderma*, can be compared.

The relationship between body mass and standard metabolic rate in helodermatid lizards is shown in figure 21. The mass exponent (0.69) is the same for both species of *Heloderma* and suggests that mass-specific metabolic rates are reduced by around 31% for each doubling in body mass. Generally, mass exponents derived from measurements of individuals *within species* are more variable and usually lower than 0.80 (the value obtained from comparisons of adults *among species*; Andrews and Pough 1985; Chappell and Ellis 1987; Thompson and Withers 1997a). For *Heloderma*, a mass exponent lower than 0.80 may be partly explained by the elevated metabolic rates shown by juveniles (perhaps associated with rapid growth), which tend to flatten the slope of the regression line and lower the mass exponent (Beck and Lowe 1994). When only adults are considered, the mass exponent for *Heloderma* is not significantly different from 0.80 (Beck and Lowe 1994).

Although the degree to which the growth in juveniles translates to increases in metabolic rate is uncertain (Nagy 2000; Beaupre and Zaidan 2001), several factors other than body mass may influence metabolic rates of reptiles. Standard metabolic rates are known to vary tremendously among different families of lizards and snakes (Andrews and Pough 1985; Chappell and Ellis 1987; Lillywhite 1987; Thompson and Withers 1997a; Bedford and Christian 1998). Evolutionary relationships help explain some of this variation in standard metabolic rate (Andrews and Pough 1985). For example, boas and pythons tend to have lower metabolic rates than other snake families (Chappell and Ellis 1987; Bedford and Christian 1998). Metabolic rate also appears to be influenced by ecological factors. Lizards and snakes that forage actively and show greater general levels of activity tend to have higher standard metabolic rates, even within the same family (Andrews and Pough 1985; Thompson and Withers 1997a). Species that are reclusive, fossorial, restricted in their foraging areas, or inhabit low-productivity environments tend to have lower metabolic rates than other species (Mautz 1979; Putnam and Murphy 1982; Kamel and Gatten 1983; Andrews and Pough 1985; Mautz and Nagy 2000). Within the Varanidae, the sister group to the Helodermatidae, the more sedentary species tend to have lower standard metabolic rates (Thompson and Withers 1997a). Ecological factors, as well as evolutionary relationships, appear to be important in influencing metabolic rates of lizards and snakes (Andrews and Pough 1985; Chappell and Ellis 1987; Thompson and Withers 1997a).

How do metabolic rates of *Heloderma* compare with other groups? Standard metabolic rates of helodermatid lizards are less than half of what would be predicted based on the pooled equation from Andrews and Pough (1985). They are only about half those of other reclusive predators and are even below those of fossorial lizards, the ecological category determined by Andrews and Pough (1985) to have the lowest metabolic rates (fig. 22). In fact, the standard metabolic rates of helodermatid lizards are among the lowest of any lizard measured (Beck and Lowe 1994). Metabolism in many other lizards and snakes undergoes daily rhythms that may coincide with normal periods of activity (Bennet and Dawson 1976; Feder and Feder 1981). Although Gila Monsters have a well-defined circadian clock (Lowe et al. 1967), they do not appear to show predictable circadian fluctuations in metabolic rate (Beck and Lowe 1994), perhaps because they are infrequently active, or because their timing of activity is variable (see chap. 5).

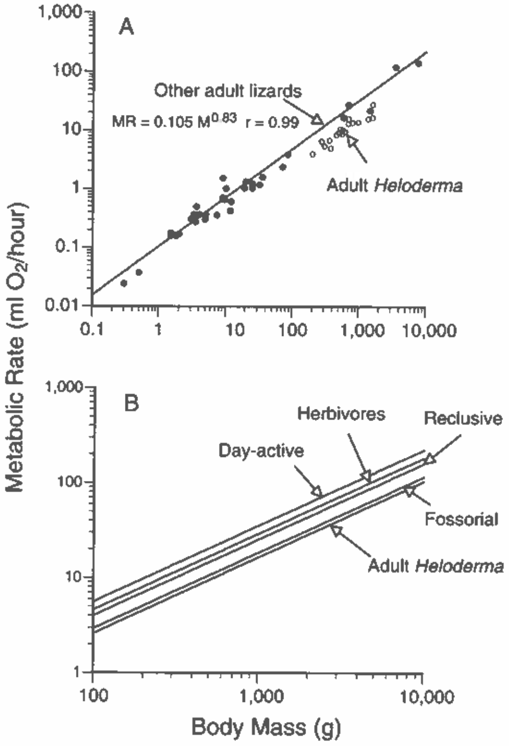


FIGURE 22. Adult helodermatid lizards have resting metabolic rates that are less than half what would be predicted based on other lizards (A) and are even lower than other groups known to have low metabolic rates, such as reclusive and fossorial species (B). After Beck and Lowe 1994.

What is the significance of a reduced SMR for *Heloderma*? An important benefit of a low SMR is conservation of energy during periods of inactivity. Energy expenditures during inactivity presumably are a substantial portion of the annual energy budgets of all animals, not just reclusive predators. A reduced SMR during periods of inactivity, therefore, might be beneficial to any species regardless of ecological factors such as activity levels and foraging behavior. However, because species with lower levels of activity spend a relatively greater portion of their lives inactive, and feed less often than their more active counterparts, the relative benefits from reduced SMR should be greater for reclusive species. In some populations, helodermatid lizards allocate only between 70 and 130 hours/year to surface activity (Beck and Lowe 1994; chap. 5) and remain resting in shelters the remainder of the time. (It should also be noted, however, that in other populations Gila Monsters show much greater levels of activity; D. F. DeNardo, pers. comm.; chap. 5). A reduced metabolic rate during the extensive periods that helodermatid lizards spend inactive constitutes a considerable energy savings, and it contributes to their ability to exploit a rare and patchy food source (vertebrate nests) upon which few other reptiles specialize (see chap. 7). The effects of temperature also likely play an important role.

EFFECTS OF TEMPERATURE ON METABOLIC RATES

Metabolic rate, like most physiological processes, slows with a decrease in temperature. The change in the rate of a physiological process caused by a 10°C change in temperature is called the Q_{10}. A twofold decrease in metabolic rate caused by a 10°C drop in temperature would have a Q_{10} of 2; a threefold decrease translates to a Q_{10} of 3; and so on. In general, a rise of 10°C causes metabolic rate, along with many other physiological rate processes, to double (i.e., $Q_{10} = 2$; Schmidt-Nielsen 1983).

We can now address the issue, brought up earlier, of how body temperatures affect energy conservation in helodermatid lizards. Figure 21 shows that between 25°C and 15°C, metabolic rate of helodermatid lizards drops threefold (i.e., $Q_{10} = 3$). The energetic implication is that as temperature decreases, energy consumption by Gila Monsters and Beaded Lizards falls even more than the norm (i.e., threefold, rather than twofold, with a 10°C drop in temperature). Because helodermatid lizards spend a good deal of the year at body temperatures below 25°C (for *H. horridum*) or 20°C (for *H. suspectum*), such periods translate into considerable energy savings (see below).

At lower temperatures (i.e., 15°C), *Heloderma* may also slip into extended periods of apnea during which their rate of breathing is reduced to only one to three breaths per minute. During these periods, lizards appear to be in a state of torpor and metabolic rate is reduced well below their already-low standard metabolic rate (Beck 1991).

The Tegu Lizard *(Tupinambis merianae)*, which inhabits seasonal savanna habitats throughout South America, shows similar episodic patterns of breathing at reduced body temperatures (i.e., 17°C; Andrade and Abe 1999a). During the dry and cold winters in southeastern Brazil, Tegus retreat to subsurface refugia where they remain dormant for 4 to 5 months at temperatures around 17°C (Andrade and Abe 1999a). Periods of torpor and reduced frequency of ventilation during winter result in optimizing the energy devoted to breathing in Tegu Lizards (Andrade and Abe 1999a) and may reduce their energy costs during dormancy. Some species of small varanid lizards also show extended periods (up to 137 minutes) of no gas exchange that may be associated with reduced rates of pulmonary water loss (Thompson and Withers 1997b). Perhaps such periods of reduced ventilation serve to conserve energy and water in helodermatid lizards as well.

MAXIMAL METABOLIC RATES

The low standard metabolic rates of helodermatid lizards may not be surprising, given that other groups of inactive reptiles also tend to have low standard metabolic rates. Their exceptional metabolic rates during activity, however, are surprising.

As oxygen demands increase during activity, the threshold at which an animal switches from oxidative (i.e., aerobic) to nonoxidative (i.e., anaerobic) metabolism corresponds to its aerobic capacity. Once its aerobic capacity is reached, a lizard begins rapidly accumulating lactic acid in its tissues and cannot sustain activity for much longer (Gleeson 1991). Aerobic capacity can be measured as the maximal rate of oxygen consumption (VO_2max) achieved while a lizard is running on a treadmill (see John-Alder et al. 1983; Beck et al. 1995). Aerobic capacities vary considerably among lizards, but it is believed that lizards showing high levels of activity tend to have higher aerobic capacities than more sedentary species (Bennett 1982, 1983; Thompson and Withers 1997a). This pattern can be observed in the varanid lizards, whose relatively high aerobic capacities tend to be correlated with high levels of activity. Helodermatid lizards, on the other hand, show relatively little activity (chap. 5). Yet, at 25°C, *H. suspectum* has a VO_2max of 3.08 $mlO_2/(g^{0.73}/hour)$, which is the highest value reported for any lizard at this temperature (John-Alder et al. 1983). At 31°C, which is closer to their activity temperature, helodermatids still show among the highest aerobic capacities of lizards (Beck et al. 1995).

Helodermatid lizards also have a high factorial aerobic scope, which is the ratio of VO_2max to standard metabolic rate. Most amphibians and reptiles show a factorial aerobic scope around 10 (i.e., VO_2max is reached at levels of oxygen consumption about 10 times their standard metabolic rates; Pough et al. 2004). The factorial aerobic scope for *Heloderma* is 30.4, which is among the highest measured for any lizard (Beck et al. 1995). In varanid lizards (*Heloderma*'s closest living relatives), factorial aerobic scope scales with body size and ranges from 9 in larger species to 35 for the smallest species measured (Thompson and Withers 1997a). Varanid species within the size range of adult *Heloderma* have factorial aerobic scopes ranging from 9 to 11 (Thompson and Withers 1997a), which are only about one-third that of *Heloderma*.

In addition to high aerobic capacities and a large factorial aerobic scope, helodermatid lizards also show great endurance when walking at submaximal speeds on a treadmill. At 1.0 km/hour, they can continue walking for an average of 16 minutes, which is longer than expected for a lizard of similar size (Beck et al. 1995). At 0.8 km/hour Gila Monsters continue walking for an average of 30 minutes, and at this pace Beaded Lizards can essentially walk indefinitely. One Beaded Lizard walked at 0.8 km/hour for over 3 hours and 40 minutes without tiring before its trial was finally terminated (Beck et al. 1995). In nature, however, helodermatid lizards forage at a pace less than one-third that which they are able to sustain on a treadmill (Beck et al. 1995; chap. 5).

The exceptional aerobic and endurance capacities of helodermatid lizards present us with another paradox. Recall that *Heloderma* do not run fast and spend less than 10% of their time engaged in physical activity (chap. 5). Why would such relatively inactive lizards show such remarkable abilities for activity? One answer might lie in their evolutionary history. Because the Helodermatidae shares a more recent common ancestor with the Varanidae than with other lizards, its high aerobic capacity may be a result of its history, a plesiomorphy inherited from its ancient varanoid stock (see chap. 2). However, *Heloderma* and *Varanus* diverged over 70 million years ago (chap. 2), which seems a very long time to retain an ancestral trait if it showed no current adaptive significance. As noted above, many varanid lizards are active foragers, and their high aerobic capacities have been interpreted as adaptations to high levels of activity (Bennett 1982, 1983; but see Gleeson 1981). Some varanid lizards, however, are also relatively sedentary (Pianka 1969; Greene 1986). For example, *V. gilleni* and *V. caudolineatus*, secretive species found beneath the bark of trees in central and western Australia, exhibit foraging behaviors that are not likely to require a high aerobic capacity (Pianka 1969; Bickler and Anderson 1986; Thompson 1993). Yet both of these *Varanus* species show very high aerobic capacities and a large factorial aerobic scope. It does not seem, therefore, that evolutionary relationships can sufficiently explain the high aerobic capacities of sedentary lizards.

Another approach to this paradox is to consider the relationship between high aerobic capacities and male combat behaviors. Male helodermatid lizards perform strenuous combat rituals that may last for several hours. In Utah, Arizona, and Nevada, male–male combat occurs in spring near shelters where males pair with females. These fights are tests of dominance between males attempting to retain (or gain) access to females. The apparent objective is to force the opponent to the ground and to remain atop him throughout a series of intensive, ritualistic bouts (see chap. 8). The lizard that consistently ends up on the bottom retreats from the fight, whereas the winner appears to maintain access to a breeding territory or a shelter housing a female. The winner, therefore, may increase his access to females and his probability of mating. Winners of male–male combat interactions in other lizards and snakes may have greater access to females and a higher probability of mating (Carpenter and Ferguson 1977; Gillingham 1987). In captive Gila Monsters, winning a combat encounter with another male often serves as a stimulus for copulation, whereas losers are less likely to breed (Gates 1956; Rundquist 1992; Strimple 1995; J. Branham, pers. comm.). Male *Heloderma* with superior strength and endurance may more frequently emerge victorious during combat rituals and thereby enjoy greater reproductive success. A high VO_2max may also be advantageous in these physically taxing encounters, a result supported by the finding that male *Heloderma* have significantly higher aerobic capacities than females (Beck et al. 1995). This result further suggests that sexual selection may have acted on aerobic capacities through male–male combat rituals in helodermatid lizards (Beck et al. 1995). Helodermatid lizards also show sexual dimorphism in other morphological traits related to male combat (chap. 8; Gienger and Beck in review).

Interestingly, both *V. gilleni* and *V. caudolineatus*, who, like *Heloderma*, exhibit foraging behaviors that seem unlikely to require a high aerobic capacity, also perform strenuous combat postures that are very similar to those of Beaded Lizards (J.B. Murphy and Mitchell 1974; Carpenter et al. 1976; Beck and Ramírez-Bautista 1991; Thompson et al. 1992). These two species have factorial aerobic scopes of 28.4 and 35.0, respectively (Bickler and Anderson 1986; Thompson and Withers 1997a), which, along with *Heloderma* (30.4), are the three highest factorial aerobic scopes recorded for lizards. Other members of the Varanidae also exhibit strenuous grappling behaviors during male fighting (J.B. Murphy and Mitchell 1974; Carpenter et al. 1976; Auffenberg 1981a, 1988). Ritualized grappling postures are more pervasive in the Varanidea than in other lizard taxa (Carpenter and Ferguson 1977; Beck and Ramírez-Bautista 1991). Thus, the high aerobic capacities of helodermatid lizards, and possibly some of their varanid relatives, may be as much a result of selection for endurance during strenuous male combat rituals as they are adaptations for foraging activity. This hypothesis needs to be further tested in varanid lizards.

COST OF LOCOMOTION

The metabolic cost for a helodermatid lizard to walk at a pace of 0.4 km/hour at the mean activity temperature of 30°C is described by the following equation (from Beck et al. 1995):

$$\log_{10} VO_2\ (\text{ml } O_2/\text{hour}) = 0.839 + 0.564 \log_{10} \text{Body Mass (g)}$$

The actual foraging pace in nature may be a bit slower than 0.4 km/hour, although it varies considerably (see chap. 5). Based on equation (1), a 500-g *Heloderma* would have a sustained VO_2 of 229.7 ml O_2/hour walking at a pace of 0.4 km/hour. This translates to a cost of transport of 574.3 ml O_2/km or 1.15 ml O_2/g/km for a 500-g *H. suspectum* (or 0.94 ml O_2/g/km for an 800-g *H. horridum*). This cost of locomotion for *Heloderma* is relatively low among lizards but still falls within the 95% confidence limit calculated from 19 lizard species in 7 families (see Equation 3 of John-Alder et al. 1986).

ASSIMILATION EFFICIENCY

Assimilated energy is the portion of energy ingested that is actually digested and assimilated into the body for use in maintenance or growth. The remainder is egested as waste in the feces. Assimilated energy expressed as a percentage of the original energy content of the food item is called the assimilation efficiency. Assimilation efficiencies vary among food items and generally range from 70% to 90% for insectivorous lizards (Iverson 1982). For Gila Monsters eating newborn rats, assimilation efficiencies range from 69.5% to 84.8% (mean = 76.5%; Beck 1986). Assimilation efficiencies of 90.6% have been recorded from Gila Monsters eating laboratory mice (Wegscheider 1998).

ENERGY BUDGETS

An energy budget is a quantitative summary of an organism's energy expenditures over a day, season, or year (McNab 2002). Among the most accurate ways to estimate energy expenditures of animals in the wild is to inject water containing the radioisotopes ^{2}H and ^{18}O into the body and trace the fate of the isotopes. By monitoring the comparative rates of disappearance of the two isotopes, one can obtain an accurate estimate of water turnover and energy expenditures from free-living animals (Nagy 1992). This method, known as the doubly labeled water technique, is being applied to a population of Gila Monsters in the Mohave Desert (C.M. Gienger, C.R. Tracy, and K.A. Nagy, unpublished data). Until results of that study are available, however, we can use current knowledge of the metabolic costs of activity and rest and, from chapter 5, estimates of the time devoted to rest and activity, to construct a time–energy budget for helodermatid lizards. Table 10 gives a comparison of the estimated annual maintenance energy expenditures for a Gila Monster from Utah compared with a Beaded Lizard from Jalisco. These estimates do not include energy expenditures associated with growth or reproduction, and so they represent the minimum energy required to maintain a constant body mass over a year.

For both Beaded Lizards and Gila Monsters these energy expenditures are low. A 500-g Gila Monster uses approximately 2,116.5 kJ (or 506 kcal) per year to satisfy it maintenance energy demands; an 800-g Beaded Lizard uses approximately 3,774 kJ (902 kcal, table 10). Helodermatid lizards spend a relatively large fraction of their time resting (at SMR), which, interestingly, translates to a smaller fraction in terms of energy because their standard metabolic rates are so low. Conversely, a tiny fraction of time spent active translates to a relatively greater proportion of energy because activity is comparatively costly. Therefore, for individuals that spend more time active, maintenance energy costs will show a disproportionate increase. Nevertheless, *Heloderma* from both Utah and Jalisco allocate a relatively small proportion of maintenance energy to activity (9.0% and 10% for *H. suspectum* and *H. horridum*, respectively; see fig. 23). Other lizards that employ a "widely foraging" strategy (see chap. 7) have been found to allocate well over 35% of maintenance energy to activity (Anderson and Karasov 1981; Huey and Pianka 1981; Nagy et al. 1984). The activity energy expenditures of helodermatid lizards, therefore, are among the lowest for any lizard that must search widely for hidden prey (see chap. 7). The reader should note, however, that recent work by D.F. DeNardo in Arizona and C.M. Gienger in Nevada suggest that some Gila Monster populations show considerably greater activity, especially during July and August, than I measured either from the Utah population or from *H. horridum* in Jalisco (see chap. 5).

How do these energy expenditures translate to food requirements? Assuming an assimilation efficiency of 80% (Beck 1986; Wegscheider 1998), a Gila Monster would need to take in 2,646 kJ of food each year to satisfy its maintenance energy demands. Assuming the energy content of prey averages 20.6 kJ/g (or 4.9 kcal/g), and 75.5% of total prey mass is water (Beck 1986), a Gila Monster from Utah could fulfill its annual maintenance energy demands by eating 524 g of food, or a quantity equivalent to 1.05 times its body mass. Given that wild Gila Monsters are known to eat meals equivalent to one-third of their body mass (Beck 1990; see chap. 7), annual maintenance energy demands could be met with three large meals. Based on these same assumptions, an 800-g Beaded Lizard would need to eat 935 g of food/year to meet its maintenance energy demands, a quantity equivalent to 1.17 times its body mass (see table 10).

Beaded Lizards have higher energy demands than do Gila Monsters, but this is not merely because they are larger. Recall that mass-specific metabolic rates of *Heloderma* are reduced by around 31% for each doubling in

TABLE 10

Maintenance Energy Budgets for a Typical 500-g H. suspectum *and an 800-g* H. horridum

BODY TEMPERATURE (°C)	METABOLIC STATE	METABOLIC RATE (ML O_2/HOUR)	PERIOD	ENERGY USED kJ/YEAR	ENERGY USED kCAL/YEAR
500-g H. SUSPECTUM FROM UTAH					
15	SMR	3.20	Dec–Feb (90 days)	138.8	33.2
20	SMR	5.28	Mar, Nov (61 days)	155.2	37.1
25	SMR	9.61	1/2 Apr–Jun; 1/2 Aug–Oct (91.5 days)	423.8	101.3
25	Alert	19.22	1/2 Apr–Jun; 1/2 Aug–Oct (91.5 days)	847.5	202.6
30	SMR	15.84	1/2 July (15.5 days)	118.3	
30	Alert	31.68	1/2 July (15.5 days)	236.6	56.5
30	Active	1.15 ml/g/km	17 km (65 hours)	196.3	46.9
			Total	2,116.5	505.9
800-g H. HORRIDUM FROM JALISCO					
20	SMR	7.67	Dec–Feb (90 days)	325.9	77.9
25	SMR	13.30	1/2 Mar–May; 1/2 Aug–Nov (107 days)	685.8	163.9
25	Alert	26.60	1/2 Mar–May; 1/2 Aug–Nov (107 days)	1,371.6	327.8
30	SMR	23.01	1/2 Jun–July (30.5 days)	338.2	80.8
30	Alert	46.02	1/2 Jun–July (30.5 days)	676.4	161.7
30	Active	0.94 ml/g/km	25 km (121 hours)	375.8	89.8
			Total	3,773.7	901.9

NOTE: Body temperatures are derived from field studies (see fig. 19). Standard metabolic rates (SMR) are derived from Beck and Lowe 1994 (also see fig. 21). During nondormant months, time in shelters is assumed to be split evenly between SMR (standard metabolic rate, see text) and basal metabolic rate (resting, but alert). Metabolic rates when lizards are alert are assumed to be two times SMR. Proportion of time spent at SMR, alert, and active are estimated from observations in the field (Beck 1990; Beck and Lowe 1991). Activity metabolism is derived from equation (1) of this chapter and Beck et al. 1995. Rates of O_2 consumption converted to joules assuming 20.08 J/ml O_2 (Schmidt-Nielsen 1983).

body mass (i.e., they show a mass exponent of 0.69). An 800-g Beaded Lizard, therefore, has a resting metabolic rate only 86.6%, on a per gram basis, that of a 500-g Gila Monster at the same temperature. In addition, its mass-specific cost of transport would also be lower (table 10). Although it would have higher absolute energy demands because it is bigger, a Beaded Lizard should be able to subsist on proportionately less energy per year than a smaller lizard, yet, in fact, they have to eat more. If we make a more direct comparison, say a hypothetical 700-g Utah Gila Monster (they occasionally get that large) and a 700-g Jalisco Beaded Lizard, we find that a 700-g Jalisco Beaded Lizard still requires about 24% more energy per year to fulfill its maintenance needs than would a 700-g Gila Monster from the Mohave Desert (fig. 23). The difference (633 kJ) amounts to an additional 160 g of food that must be eaten by *H. horridum*. This is the cost of living in the tropics, where warmer temperatures drive up metabolic costs, and where a longer activity season translates to higher activity costs (fig. 23). On the other hand, primary productivity is much greater in tropical dry forest than in the Mohave Desert and potential prey species are presumably more abundant (chap. 5). Therefore, fulfilling its greater energy demands may be a minor challenge for *H. horridum*.

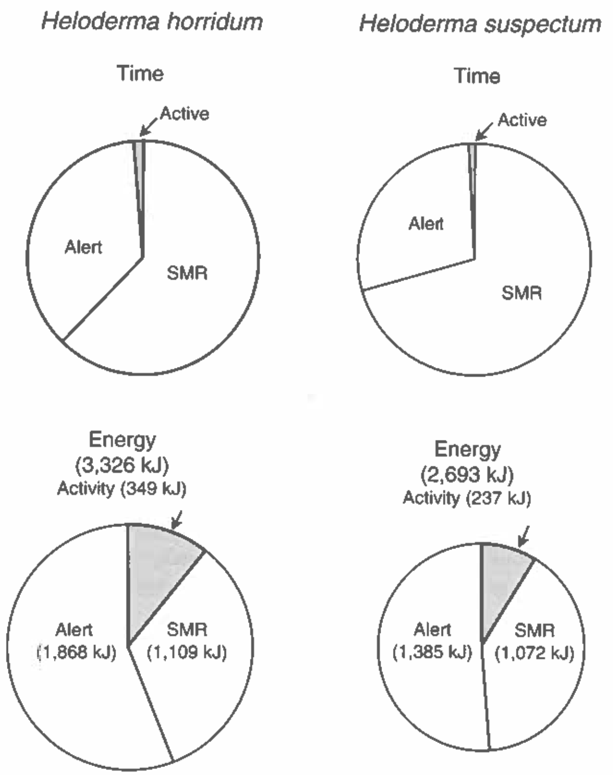


FIGURE 23. Comparison of time-energy budgets between two hypothetical 700-g helodermatid lizards. A Gila Monster from Utah uses only 80% as much energy as an equivalent Beaded Lizard from Jalisco. *Heloderma horridum* uses more energy because of its longer activity season and the warmer body temperatures it experiences in its tropical dry forest habitat.

The annual energy requirements of helodermatid lizards are comparable to those of rattlesnakes, which represent extreme examples of ectotherms as low-energy systems (Pough 1980; Beck 1995; Beaupre 1996). A 100-g Mottled Rock Rattlesnake can fulfill its annual energy demands on a prey quantity equivalent to between 113.3% and 193% of its body mass (Beaupre 1996). Sidewinder Rattlesnakes have been estimated to consume prey equivalent to approximately 220% of their body mass to meet annual energy demands (Secor and Nagy 1994).

The energy efficiencies of helodermatid lizards become much more striking when we compare them with those of a comparable-sized mammal. An 850-g Black-footed Ferret, *Mustela nigripes* (about the size of an average Beaded Lizard), must eat 1 prairie dog (approximately the same mass as the ferret) every 3 to 4 days to fulfill its energy demands (Powell et al. 1985). Over a year, therefore, a Black-footed Ferret must consume about 100 prairie dogs, or a quantity of prey equivalent to approximately 100 times its body mass. A Gila Monster requires barely 1% as much energy. Because the streamlined body of a mustelid necessitates a relatively high metabolic rate (J. H. Brown and Lasiewski 1972), the ferret may be an extreme example, but it serves to illustrate the high-energy efficiency of ectothermic predators, especially the helodermatid lizards.

FAT STORAGE AND DRINKING

Helodermatid lizards are notorious for storing energy as fat in their tails (plate 21). One need only compare most captive specimens with the typical wild Gila Monster to appreciate how rapidly tails can become rotund with regular feeding. In nature, however, tail diameter may vary considerably because a lizard gains and loses weight in association with seasonal changes in food availability and feeding. I have been astounded at how emaciated some lizards can become, only to witness an impressive comeback

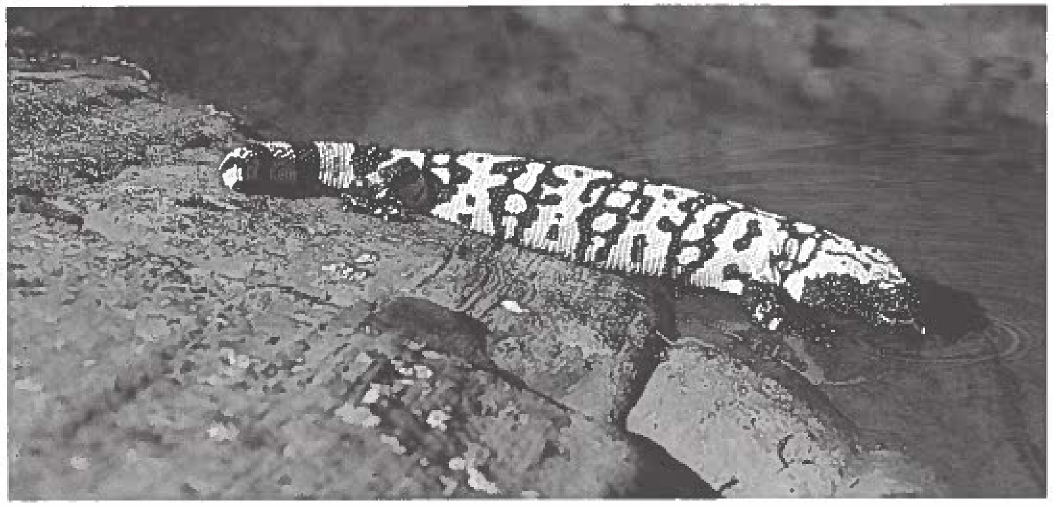


FIGURE 24. Helodermatid lizards have high rates of evaporative water loss, a trait thought to be a legacy of their tropical origins. Although they have rarely been observed to drink in nature, they may do so if given the opportunity, as shown by this wild Gila Monster drinking out of an ephemeral rain pool in southwestern Utah (photograph by D. Beck).

once a few meals are eaten. For example, one Beaded Lizard (El Flaco) I tracked in Jalisco added over 1 cm to its tail diameter between June 1986 and June 1987 (its SVL increased 11 mm, or 3%, during the same period). Tail girth also appears to be associated with hydration status, and it may increase measurably with only a modest drink of water. One Chamela Beaded Lizard gained 52 g from drinking after a modest June rain and added 10 mm to its tail circumference.

The anatomy of the tail of *Heloderma* has been investigated by Shufeldt (1890) and Schneider (1941). The tail is naturally divided into four compartments running the length of the tail, each separated by a band of muscle. Two compartments are oriented above the vertebral column and two larger ones are oriented below. Within these compartments, fat is deposited, running as "longitudinal cones of adipose tissue" (Shufeldt 1890). Less commonly known, but no less important, is that fat bodies also extend well into the body cavity, forming large deposits within the region flanking the testes, ovaries, and oviducts. *Heloderma* is thus well endowed with an impressive ability to store large quantities of energy in the form of fat in both the tail and the body cavity.

Some have suggested that fat reserves in the tail may also serve as a water source, primarily in the form of metabolic water released when fat is metabolized (Schneider 1941; Schmidt-Nielsen 1964). Bogert and Martín del Campo (1956) downplayed this possibility because as oxygen is delivered to the cells (to oxidize fat and yield metabolic water), water is also lost from the lungs during respiration. However, in *Heloderma*, air is generally not heated during respiration because body temperatures of lizards in shelters are usually similar to those of their surroundings (see above). Respiratory water losses are thereby greatly reduced in comparison to those of mammals and birds where the benefits of metabolic water are often outweighed by large respiratory water losses (Schmidt-Nielsen 1964). In addition, low respiratory rates and episodic ventilation patterns may translate to reduced rates of respiratory water loss (Thompson and Withers 1997b; Andrade and Abe 1999a). The tail as a potential water storage organ in helodermatid lizards has not been thoroughly investigated and may prove a fruitful topic for future research in how *Heloderma* endures periods of drought.

TABLE 11

Total Evaporative Water Fluxes (mg/g/hour) of Some Lizards Inhabiting Arid Environments

	BODY MASS (G)	T_a (°C)	EWL (MG/G/HOUR)
Crotaphytus collaris Collard Lizard	30	32.0	0.46
		40.0	0.73
		44.0	4.70
Dipsosaurus dorsalis Desert Iguana	48	32.0	0.86
		40.0	2.08
		44.0	3.64
Sauromalus obesus Chuckwalla	140	26.0	0.22
		40.0	0.67
		43.5	2.36
Pogona barbatus Bearded Dragon	241	30.0	0.47
		40.0	1.04
Trachydosaurus rugosus Shingle-back Lizard	315	30.0	0.67
		40.0	1.12
Heloderma suspectum Gila Monster	606	20.0	0.84
		30.0	1.57
		40.0	7.27

NOTE: The higher T_a for each species is near the upper limits of tolerance. The dramatic increase in EWL of Gila Monsters at 40°C is attributable to cloacal water loss (after DeNardo et al. 2004).

Although they are not normally exposed to perennial sources of standing water, both species of *Heloderma* occasionally drink in nature when they have the opportunity (fig. 24). And captive Gila Monsters do seem to love a good soak in the water dish. Captive *Heloderma* may even remain entirely submerged for periods of over half an hour (Larsen et al. 1969). Gila Monsters show a bradycardia response (reduced heart rate during diving) during such periods, where heart rate is reduced from 52 beats/minute when the head is out of water to 14 beats/minute after 4 minutes of submergence (Larsen et al. 1969). This response may enable them to survive submergence during a flood, but it does not mean that wild helodermatid lizards require access to permanent sources of water. Populations are frequently discovered many miles from a permanent water source. Most of the water needs of helodermatid lizards are likely met by water they consume with their prey (see chap. 7), augmented by production of water through metabolism and the occasional opportunity to drink from ephemeral rain pools.

WATER LOSS RATES

Both Gila Monsters and Beaded Lizards have long been suspected to have unusually high rates of evaporative water loss (Lowe et al. 1986; W. Porter and D. Beck, unpublished data). However, this interesting phenomenon has only recently been explored. DeNardo et al. (2004) recorded evaporative water loss (EWL) in Gila Monsters both from the lungs (i.e., ventilatory EWL) and from the skin (cutaneous EWL), as is traditionally done in studies of water loss in reptiles (Mautz 1982). However, these researchers also measured cloacal EWL by fashioning a "diaper" that prevented moisture from leaving the cloaca. They found that *H. suspectum* had total rates of evaporative water loss that were more than double those of other lizards inhabiting arid environments (DeNardo et al. 2004; table 11). At thermally stressful temperatures (approaching 40°C), DeNardo et al. (2004) found that EWL increased dramatically in Gila Monsters, a result that has also been observed to a lesser extent in some other lizards (table 11). However, this increase in EWL was not from cutaneous or ventilatory fluxes (unlike other lizards, *Heloderma* do not pant at high temperatures) but was attributable to evaporative water lost from the cloaca. Even more interesting, however, was that at high temperatures, the elevated rate of cloacal water loss was associated with a decrease in body temperature of nearly 2°C over controls (fig. 25). This suggests a means of evaporative cooling that has not previously been observed in lizards (DeNardo et al. 2004).

It appears that, rather than pant when they are thermally stressed as most lizards do, Gila Monsters lose large quantities of water from the cloaca, a response which may actually help them temporarily reduce their body temperature. In critical thermal situations, this response may help give a little more time to escape stressful temperatures and avoid crossing a dangerous threshold, near the critical thermal maximum, when coordinated escape may no longer be possible. Gila Monsters are unique in that EWL rates at high temperatures are considerably higher than even those of panting lizards and in that the source of this dramatic increase in EWL is the cloaca (DeNardo et al. 2004).

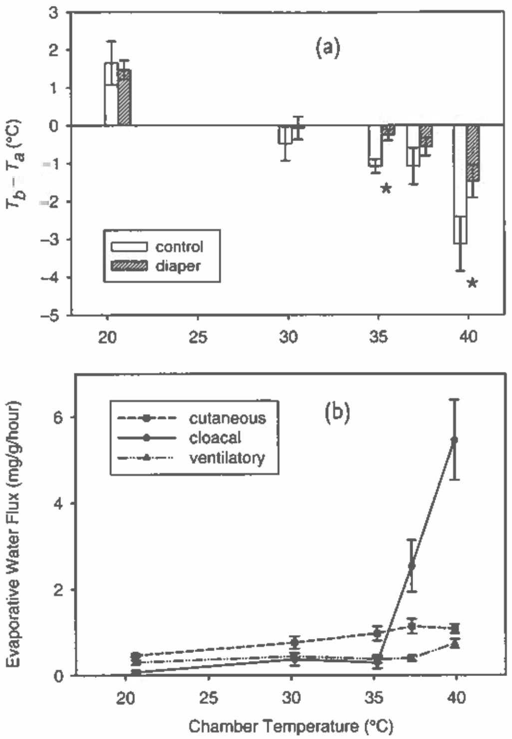


FIGURE 25. Relationship between cloacal evaporative water loss (EWL) in Gila Monsters and body temperature. (A) Differences between body temperature (T_b) of Gila Monsters and ambient chamber temperature (T_a) at five experimental temperatures show that at higher temperatures Gila Monster T_bs are suppressed below ambient. This coincides with the temperatures at which cloacal EWL is dramatically elevated (B; after DeNardo et al. 2004).

Evaporative water loss in *H. suspectum* more closely matches that of lizards from semiarid or mesic environments. And when body size is taken into consideration (which is inversely related to EWL rate), EWL in *H. suspectum* appears considerably higher than in other lizards regardless of habitat type (Mautz 1982; DeNardo et al. 2004).

Some researchers have suggested that high rates of water loss in helodermatid lizards may be a carryover from their varanoid ancestors, many of which inhabited more mesic environments (Lowe et al. 1986; chap. 2). It seems odd, however, that such a legacy would be retained for so many millions of years. At critically high body temperatures, the ability to cool via EWL from the cloaca may be adaptive. But high cutaneous water loss rates at other temperatures seem puzzling for lizards that inhabit hot deserts and tropical dry forests and that show an activity peak near the hottest, driest time of year. In nature, how do helodermatid lizards cope with their high EWL rates? Because water loss decreases as temperature falls, *Heloderma*'s relatively low activity temperature may be one way of coping with high rates of evaporative water loss, as could be switching to greater nocturnal activity during the hottest part of the summer. Gila Monsters may also cope with high rates of EWL by selecting cooler, more humid microhabitats, especially during hot, dry periods (Beck and Jennings 2003). Table 12 shows mean temperatures within shelters used by Gila Monsters in southwestern New Mexico. Burrows used during the summer tend to be cooler throughout the year than other shelter types. Obviously, in order to understand the unique physiology of helodermatid lizards, we must consider their use of habitat and patterns of activity.

TABLE 12

Gila Monster Shelter Temperatures in Southwestern New Mexico during 1995–1996

	SUMMER MONSOON BURROWS				ALL SHELTER TYPES			
	MEAN °C	MEAN °F	SD °C	SD °F	MEAN °C	MEAN °F	SD °C	SD °F
Jan	9.2	48.5	2.7	4.9	12.0	53.6	3.5	6.3
Feb	12.7	54.9	2.6	4.6	14.0	57.2	3.1	5.5
Mar	13.3	55.9	2.9	5.3	16.1	61.0	3.4	6.2
Apr	17.6	63.7	3.5	6.3	19.3	66.8	3.6	6.5
May	23.8	74.8	3.4	6.1	24.5	76.1	2.2	4.0
Jun	27.6	81.7	3.1	5.5	28.7	83.7	1.5	2.7
Jul	27.8	82.0	2.2	4.0	28.9	84.1	3.0	5.4
Aug	27.2	81.0	3.1	5.6	29.1	84.4	4.1	7.3
Sep	26.1	78.9	2.9	5.2	26.3	79.3	4.8	8.6
Oct	23.2	73.8	3.8	6.8	23.9	75.0	3.4	6.2
Nov	18.6	65.5	2.0	3.7	19.0	66.3	2.2	4.0
Dec	11.9	53.5	4.8	8.7	12.7	54.9	4.4	7.9

NOTE: Means of one reading/hour, 24 hours/day; 27 total shelters; 9 summer monsoon shelters (R. Jennings and D. Beck, unpublished data). Burrows used during the wet summer monsoon tend to be cooler throughout the year than other shelter types.

CHAPTER 5

Habitat Use and Activity Patterns

HABITAT IS THE PLACE IN nature where an organism can fulfill its various resource demands (energy, water, shelter) and where environmental conditions allow the individual to maintain homeostasis. Habitat must provide microenvironments that allow an animal to avoid exceeding its limits of physiological tolerance (chap. 4). In addition, habitat must be free of biological factors, such as predators, competitors, or disease organisms, which preclude survival of the population. Individuals may be eliminated from the population by predators and disease, but, in a suitable habitat, the population will persist. Such physical and biological factors that determine habitat suitability are numerous and complex and, therefore, poorly understood for most organisms.

Complicating our understanding of habitat use are the changing resource demands of the individual and the fluctuating environment it inhabits. As helodermatid lizards grow and mature, for example, the energy and microenvironmental resources they require also change, which, in turn, affects how they use habitat. Juveniles may choose different shelter types, or different times to be active, than do adults. Eggs require a different microenvironment in which to develop than do juveniles or adults. Resource demands also change with the seasons. As mature individuals progress through seasonal reproductive cycles—as they seek, court, and pair with mates, or look for appropriate nest sites—so too do their energy needs and microhabitat requirements change. Habitats used by *Heloderma* show great spatial heterogeneity and pronounced seasonal variability in precipitation, temperature, and availability of resources. The suitability of particular microhabitats, therefore, also changes with the seasons, as do the risks of exposure to harsh surface conditions (and predators). A south-facing slope may be an ideal place to overwinter, but it becomes inadequate, even hostile, during the hot, dry summer. Suitable winter shelters may be distant from good summer sites, and favorable foraging areas may be far from good nest sites; travel among these areas may expose a lizard to overheating, desiccation, and predators.

Habitat use and activity patterns, therefore, constitute the responses shown by helodermatid lizards to their changing resource demands and to the temporal and spatial variability of their habitats. An understanding of how animals use habitats—what microenvironments they frequent, their daily and seasonal timing of activity, and how far they travel—can tell us much about the physical and biotic factors that define habitat suitability. In this chapter, we'll seek such an understanding for helodermatid lizards. I'll describe the types of macrohabitats, or biotic communities, in which these lizards are found and then examine how Gila Monsters and Beaded Lizards utilize specific features (microhabitats) within those biotic communities. Finally, I'll summarize patterns of activity and movement within their habitats and consider how activity patterns might vary in relation to season and locality.

HABITAT TYPES

A discussion of habitat use requires a familiarity of the habitat types in which helodermatid lizards are found. For this discussion, I regard *habitat type* to be synonymous with *biotic community* (Lowe 1964), which is a major ecological assemblage based primarily on diagnostic plants found therein. The biotic communities in which *Heloderma* occur include seasonally dry forests, grasslands, thornscrub, and deserts distributed from the tropics of Guatemala and Mexico to temperate regions of the southwestern United States (see chap. 2 for a summary of geographic distribution).

BEADED LIZARD HABITATS

TROPICAL DRY FOREST

Heloderma horridum is a lizard of tropical dry forest, in fact, more so than *H. suspectum* is a denizen of the desert (plates 2 and 22). Tropical dry forest is a transitional biotic community falling along the continuum between semidesert grassland/savanna and wet tropical forest (Murphy and Lugo 1986). Tropical dry forest (TDF) goes by a number of names, including seasonally dry tropical forest, tropical deciduous forest, thorn forest, and monsoon forest, among others (see Rzedowski 1978; Gentry 1982; P. G. Murphy and Lugo 1986; P. S. Martin and Yetman 2000). Neotropical dry forests extend from Mexico to Argentina and can be geographically divided into two groups: Mesoamerican (Mexico and Central America) and South American. Throughout a great majority of its range, the Beaded Lizard is associated with the Mesoamerican dry forests of western Mexico. The TDF of western Mexico covers vast regions from southern Sonora to Chiapas. These forests are largely isolated—geographically and ecologically—from other tropical forests (Ceballos 1995). Such isolation has apparently contributed to a great number of endemic vertebrate species in the TDF of western Mexico. For reptiles and amphibians, 173 species (43%) are restricted to the TDF (Ceballos 1995; García-Aguayo and Ceballos 1994).

With the exception of a small region of TDF in Guatemala (Campbell and Vannini 1988), the geographic distribution of *H. horridum* very closely matches the TDF of western Mexico (see chap. 2). So closely is *H. horridum* tied to TDF throughout its range that it too might be considered a tropical dry forest endemic. Seasonally dry tropical forest is believed to be the ancestral habitat in which *Heloderma* evolved and its life history adaptations were shaped (Stevens 1977; Pregill et al. 1986). During the Tertiary (65–2.8 million years ago), TDF occurred much farther north into western North America (Graham and Dilcher 1995), where fossil helodermatids (and other TDF organisms) have been found (see chap. 2).

A great diversity of plant life-forms is found in TDF, even more than in tropical rain forest (Medina 1995). Such life-forms include trees, vines, succulents, epiphytes, shrubs, grasses, and herbaceous plants adapted to highly seasonal precipitation. Many dry forest trees are drought-deciduous (conserving water by dropping their leaves during the dry season), and many store considerable water in their trunks and stems (Borchert 1994). Many of these trees provide impressive flowering displays during the dry season. Dominant trees include several members of the Leguminosae family, particularly the genera *Lonchocarpus* (e.g., 12 species around Chamela; Lott 1985) and *Lysiloma* (around Alamos; P. S. Martin and Yetman 2000). The nanche, or golden spoon *(Byrsonima crassifolia)*, a member of the Malpighiaceae family, is common in *H. horridum* habitat in Chiapas. Its marble-sized yellow fruits drop during the early dry season and are commonly (albeit erroneously) thought to be eaten by Beaded Lizards. Trees growing within arroyo bottoms with perennial access to subsurface soil moisture may retain their leaves throughout the year. Cacti are common in tropical dry forests, both as understory species (e.g., several species of *Opuntia*) and as large, impressive arborescent forms, such as *Pachycereus pectenarboriginum* (known as *etcho* in parts of it range).

Tropical dry forest is characterized by a several-month period of severe, even absolute, drought (Mooney et al. 1995). Periodic drought results in a situation, similar to deserts (but unlike tropical wet forests), in which potential evapotranspiration exceeds annual rainfall (P.G. Murphy and Lugo 1986). Among the driest habitats of *H. horridum* are dry forests of the middle Motagua Valley of Guatemala, with annual precipitation under 500 mm (Campbell and Vannini 1988). From an evolutionary and ecological standpoint, the dry season has been paramount in shaping adaptations of dry forest inhabitants and determining the nature of its plant communities. Most species that cannot tolerate seasonal drought are eliminated by the extended dry season. The dry season may last from five to eight months, depending on regional and annual influences. Within the range of *Heloderma*, the dry season occurs during winter and spring from November through May or June. Occasional fall and winter precipitation can be very important, however. Winter rains can originate as cool frontal storms (the equipatas of southern Sonora or cabañuelas of coastal Jalisco). Fall hurricanes can also contribute significant moisture in exceptional years.

Annual precipitation varies from around 500 mm/year to 1,500 mm/year, the majority of which falls during the 4 to 6 month wet season typically beginning in June or July and lasting through October to December. During this time, the forest is transformed from a dry, leafless landscape to a wet, green tropical forest teeming with activity (plate 23). At my study site in Chamela, Jalisco, Mexico, the dry season lasts 7 to 8 months; 80% of the mean annual precipitation of 748 mm (29.4 in.) falls during a 4-month wet season between early July and early November (Bullock 1986). On average, the seven wettest days contribute over half (53.3%) of the annual precipitation (Bullock 1986).

Temperatures in tropical dry forest generally vary more within a single day than do mean temperatures over the course of a year. For example, at Chamela, monthly mean temperatures range from near 22°C (March) to 27°C (July) whereas daily swings in July average 22°C to 32°C and in January from 15°C to 30°C (Bullock 1986). Mean maximum temperatures range from 29°C (March) to 32°C (August), and mean minimum temperatures range from 15°C (February) to 23°C (July; Bullock 1986). Freezing temperatures are extremely rare to nonexistent in tropical dry forest.

As with all biotic communities, the character of a particular tropical dry forest site is affected by regional variations in climate, soils, and topography. For example, in TDF of western Mexico, two major forest types occur (Lott et al. 1987). An upland dry-deciduous forest grows on dissected hilly terrain with numerous small drainages. Its 4–15 m-tall canopy overlays a well-developed understory of shrubs; herbaceous cover becomes dense during summer and fall months. A taller riparian semideciduous forest, developed on the larger arroyos, has a more open understory. The two habitat types are referred to by Lott et al. (1987) as upland forest and arroyo forest. They are, respectively, the "selva baja caducifolia" and "selva mediana subperenifolia y subcaducifolia" of Miranda and Hernandez (1963).

OTHER HABITAT TYPES FOR *H. HORRIDUM*

In drier sites (with annual precipitation of only 300–500 mm/year), or where soils are shallow, tropical dry forest grades into tropical thornscrub (D.E. Brown 1982), which is dominated by shrubs and shorter shrublike trees (e.g., *Acacia, Bursera, Prosopis*). Arborescent cacti (e.g., *Pachycereus, Stenocereus*) are still found, penetrating the relatively short canopy of tropical thornscrub. Beaded Lizards are largely absent from this biotic community, although they do occur rarely in thornscrub habitats bordering adjacent tropical dry forest. In wetter environments with annual precipitation over approximately 1,500 mm, and at higher elevations, tropical dry forest gives way to humid (e.g., cloud) or evergreen and/or coniferous forests in which *H. horridum* generally do not occur.

Beaded Lizards are also occasionally encountered in open savannas along the edges of cultivated fields and in open, seasonal arroyos with sandy soils, where they may forage for eggs of Spiny-tailed Iguanas that build nests in these friable environments during May. Pine–oak woodland habitats, which border tropical dry forests throughout most of its range, are also occasionally inhabited by Beaded Lizards (e.g., Schwalbe and Lowe 2000).

GILA MONSTER HABITATS

Although commonly portrayed as a desert beast, the Gila Monster is not strictly restricted to the desert and, in fact, tends to avoid the harshest desert habitats. Biotic communities inhabited by Gila Monsters include tropical thornscrub, desert grassland, southwestern desertscrub (Sonoran, Mohave, and Chihuahuan), and, more rarely, woodlands.

SINALOAN THORNSCRUB

This is a biotic community intermediate between the desert and tropical dry forest. It is wetter than the desert but drier than tropical dry forest; annual precipitation ranges from 300 to 500 mm (12–20 in.), 70% of which falls during July to September (D.E. Brown 1982). Despite its name, Sinaloan thornscrub is not confined to Sinaloa but also encompasses large regions of southern Sonora, Mexico, from sea level to over 900 m (3,000 ft) in the mountains. It is these foothill thornscrub habitats—on low hills, mesas, bajadas, and mountain slopes—that are most commonly frequented by *Heloderma*, a region earlier classified by Shreve (1951) as the "Foothills of Sonora" subdivision of the Sonoran Desert. Many biologists believe tropical thornscrub also better describes another part of the Sonoran Desert—the Arizona upland subdivision—a biome in which Gila Monsters also thrive (see below). In contrast to the Arizona upland, freezes are rare in Sinaloan thornscrub, which has a much more tropical flavor than do any of the desert habitats in which *Heloderma suspectum* occurs.

One must be wary when walking through Sinaloan thornscrub. It comprises a dense thicket of thorny subtrees and shrubs that stand between 2 and 7.5 m (6–25 ft) high. Many of these plants are drought-deciduous and have small, pinnately compound leaves and multiple trunks. Many succulents also occur in the Sinaloan thornscrub; organ pipe cactus *(Stenocereus thurberi)* and etcho *(Pachycereus pectenaboriginum)* can be locally abundant and conspicuous. Sinaloan thornscrub is particularly interesting because this is the habitat type in which both species of *Heloderma* may be found. An old record exists of a *H. suspectum* near El Dorado in central Sinaloa, in the heart of what once was Sinaloan thornscrub (chap. 2). Much of this region has been converted to agriculture, so we may never know whether Gila Monsters ranged more extensively into the thornscrub in Sinaloa or if the record is merely evidence of a spotty, rare occurrence.

SOUTHWESTERN DESERTSCRUB

Southwestern desertscrub refers to what one might consider the "typical" desert habitats found in the three major hot deserts of North America: the Sonoran, the Chihuahuan, and the Mohave deserts. Southwestern desertscrub is an arid, hot biotic community with irregular precipitation (normally less than 254 mm or 10 in. per year) harboring a variety of shrubs and/or subtrees, herbs, grasses, and succulents (see Lowe 1964; D.E. Brown 1982; Turner 1982; and Turner and Brown 1982). The term *subtree* applies to the many small trees, such as paloverde, white thorn acacia, mesquite, and ironwood, that grow in certain Sonoran desertscrub habitats (see below). These trees provide an important source of cover as well as food and shelter for a number of species on which Gila Monsters feed (chap. 7). Gila Monsters have also been observed to climb into these subtrees (Cross and Rand 1979). As for shrubs, creosote bush *(Larrea tridentata)* is the most common associated with desertscrub habitat and is, in fact, a good indicator species of southwestern desertscrub.

SONORAN DESERT HABITATS

The heartland of Gila Monster habitat is the subtropical Sonoran Desert. An important climatic feature of the Sonoran Desert region is a bimodal pattern of annual precipitation. Two rainy seasons occur: one in summer and one in winter. Summer rains tend to be more intense, convective storms, whereas winter storms tend to be gentler and longer lasting (MacMahon 1979). In the western part of the Sonoran Desert, more of the annual precipitation falls as winter rain, and in the eastern part, summer rain comprises the bulk of annual precipitation. For example, in the lower Colorado River and Gulf Coast subdivisions, annual precipitation is about 60% in winter (October–March), 40% in summer (April–September), whereas in the Arizona upland subdivision, summer precipitation approximately equals that which falls during winter. The biseasonal rainfall pattern is an important factor influencing the impressive biotic diversity of the Sonoran Desert and doubtless plays an important role in activity patterns and habitat use by Gila Monsters.

Another important contributor to the biotic diversity of the Sonoran Desert is its tremendous topographical relief. Located within the Basin and Range province, numerous mountain ranges contribute elevational complexity that, in turn, increases the diversity of climate regimes and microhabitats. A short trip up a typical mountain range in the Sonoran Desert allows one to enter at least three different life zones and five different biotic communities (Lowe 1964). This availability of diverse habitats within a relatively short distance obviously influences the distribution and abundance of many organisms that make their home in the Sonoran Desert, including *Heloderma*. Another important factor in the biotic diversity of the Sonoran Desert is its proximity to the neotropics, a rich source of biological diversity in itself. Many of the species inhabiting the Sonoran Desert region are tropical in origin (Axlerod 1979; Schwalbe and Lowe 2000).

Because of its diversity in climate and topography and its considerable geographic extent, up to seven subdivisions have been described for the Sonoran Desert (Shreve 1951; Shreve and Wiggins 1964). Five of these subdivisions are recognized today as Sonoran desertscrub (Turner and Brown 1982; Dimmitt 2000), and Gila Monsters are found in four of them: Arizona upland, lower Colorado River valley, central Gulf coast, and plains of Sonora. *Heloderma* is absent from the Vizcaino subdivision of Baja California.

ARIZONA UPLAND The subdivision of the Sonoran Desert most commonly frequented by Gila Monsters is the Arizona upland (Lowe et al. 1986). This is the classic Sonoran Desert habitat, dominated by creosote bush and a diversity of other shrubs, paloverdes and other subtrees, and saguaros and many other cacti (plate 24). Many desert biologists have argued that Arizona upland is really not a desert at all but is more closely related to subtropical thornscrub (Turner and Brown 1982). It is "the best watered and least desertlike desertscrub in North America" (Turner and Brown 1982; Dimmitt 2000). They make a good case. Tucson, Arizona, for example, in the heart of Arizona upland, receives 11 in. (279 mm) of rainfall per year. It looks and feels more like a depauperate northern extension of subtropical foothill thornscrub (described above) than it does a desert. Arizona upland habitats are often strikingly beautiful (plate 24), and their diversity of plant species and life-forms is equally impressive. The vast majority of this region is on multidissected sloping terrain and broken ground, hence the name *Arizona upland*. Arizona upland habitats, therefore, tend to possess considerable topographical relief and often have relatively coarse soils associated with bajadas (the gently sloping alluvial skirt of a mountain range). They also tend to have a diversity of potential prey species and shelter sites, including rocky crevices, burrows, and pack rat middens (see Microhabitat Use, below). Gila Monsters are found throughout the Arizona upland inhabiting rocky slopes as well as arroyos and flatlands. Rocky slopes and outcrops are often used as overwintering sites.

LOWER COLORADO RIVER VALLEY The lower Colorado River valley is the largest and most arid subdivision of the Sonoran Desert (Turner and Brown 1982). This is a more open, sandy desert than is the Arizona upland. Topographical relief tends to be lower and vegetation more sparse. The dominant plants include the common shrubs creosote bush *(Larrea tridentata)* and white bursage *(Ambrosia dumosa)*, which may form nearly pure stands for many square miles. Subtrees (e.g., paloverde, mesquite, ironwood), saguaros and ocotillos tend to be restricted to runnels where runoff water provides the additional moisture needed for these species. Within the lower Colorado River valley subdivision of the Sonoran Desert, Gila Monsters are more frequently encountered in transitional, or ecotonal, areas, between the creosote bush–white bursage series and the paloverde–cactus series of the Arizona upland, where topographical relief tends to be greater. These areas generally show greater plant cover and primary productivity and, in turn, a greater availability of potential prey species. Gila Monsters are less frequently encountered in the more open, sparse creosote bush–white bursage series. Rodent burrows and pack rat middens are important microhabitat features of this habitat type, where reduced topographical relief provides fewer options for retreat into rocky shelters. Vast regions of the lower Colorado River valley in California and northern Baja California are not inhabited by Gila Monsters.

CENTRAL GULF COAST AND PLAINS OF SONORA Less is known about habitat use by Gila Monsters in the central Gulf coast and plains of Sonora subdivisions of the Sonoran Desert. The central Gulf coast includes a region along the coast of Sonora (and Baja California) that is exceptionally diverse in succulents and notable for a relative absence of a shrub layer (Turner and Brown 1982). In Baja California, Gila Monsters are absent from this subdivision, and for many years range maps did not show Gila Monsters occurring within the central Gulf coast of Sonora, Mexico either, probably because it is so remote that few specimens had been reported there. However, Gila Monsters have been found in the central Gulf coast subdivision along the low desert mountains and adjacent bajadas in coastal Sonora (B. Martin, pers. comm.; fig. 6). The particular microenvironments used by Gila Monsters in the central Gulf coast region are likely similar to those used in other habitat types.

The plains of Sonora is a region of undulating terrain that is transitional between Arizona upland and thornscrub habitats occurring farther south. It is characterized by relatively open stands of subtrees, primarily mesquites, ironwoods, and paloverdes. These plants undoubtedly provide important cover and resources for both Gila Monsters and their prey species. Gila Monsters are commonly encountered in this biotic community; many are picked up each year in the hills and arroyos surrounding Hermosillo, Sonora (plate 18).

DESERT GRASSLAND

Desert grassland (also known as *semidesert grassland*) is a transitional habitat type between desertscrub and grassland, and, within the Sonoran Desert region, it is a biotic community in which Gila Monsters thrive (plate 25). Semidesert grassland habitats frequently occur along the foothills of southwestern "sky island" mountain ranges (between 600 and 1,550 m, or 2,000–5,000 ft) where temperatures are a little cooler and rainfall a little higher. Second only to Arizona upland, these communities are a preferred habitat type for *H. suspectum suspectum*. The desert grassland habitats where Gila Monsters are most frequently seen tend to be hilly and relatively rocky and contain a mix of desert elements, such as cacti, ocotillos, some subtrees (catclaw, mesquite, hackberry) and shrubs (e.g., the occasional creosote bush, snakeweed, desert broom) as well as grasses. Gila Monsters generally avoid pure grassland; they prefer the grassland–desert ecotone.

MOHAVE DESERT HABITATS

The Mohave Desert is a transitional region wedged between the Great Basin to the north and the Sonoran Desert to the south. Many biologists regard the Mohave as a transitional extension of the Sonoran Desert, but a long history of reference to the Mohave as a distinct desert entity seems to have prevailed (MacMahon 1979; Turner 1982). Nevertheless, the Mohave Desert does have some traits that distinguish it from other North American deserts. Rainfall is scant in the Mohave Desert, generally ranging between 65 and 195 mm (2.5–7.7 in.) per year. Similar low values occur in other deserts, but what sets the Mohave apart is the timing of precipitation (primarily in winter) and its combination of low winter and high summer temperatures (Turner 1982). A few sites in the eastern Mohave receive a significant portion of their annual precipitation in summer, but the majority of the region is dominated by a winter precipitation regime. Winter storms in the Mohave tend to be longer lasting and gentler than the convective summer storms of the Sonoran Desert.

Another characteristic feature of the Mohave Desert is the presence of the Joshua tree *(Yucca brevifolia)*, which is commonly referred to as an *indicator* species of Mohave desertscrub. Joshua trees tend to be found in microclimates having colder winter temperatures and in areas where soils are coarser, such as along middle-to-upper bajadas. Much of the Mohave Desert is devoid of Joshua trees, however, and characterized by open valleys containing miles of creosote bush and white bursage. Along upper elevations of its transition with the Great Basin, shadscale *(Atriplex confertifolia)* or blackbrush *(Coleogyne ramosissima)* may dominate the Mohave desertscrub. In many of the lower valleys with saline or very dry soils, saltbush (*Atriplex* sp.) takes over as the dominant shrub. Gila Monsters are generally absent from both blackbrush and saltbush communities.

At its southern limits, the Mohave meets the Sonoran Desert in a rather fuzzy boundary, but in the north, along its transition with the Great Basin and California coastal chaparral, the boundaries are sharply defined. Elevational gradients produce a distinct margin between the Mohave and Great Basin deserts. Interestingly, it is along such higher-elevation transition areas, in southwestern Utah and southeastern Nevada, for example, that some of the most productive habitat for *H. suspectum cinctum* can be found in the Mohave Desert. In these areas, Gila Monsters may be associated with rocky terrain and frequently use rocky shelters associated with sandstone or granite outcrops. Some of these habitats are stunningly beautiful; sculptured rose, pink, and white sandstone cliffs towering over sandy salmon-colored valleys (plates 7 and 26). During spring and early summer, individuals may move out of the rocks and into less steep, sandy areas to forage. Gila Monster tracks, easily identified in the sand, often tell a story of such travels taken by foraging lizards (chap. 1). In California, *H. s. cinctum* has been recorded from rocky slopes in isolated desert mountains (chap. 2) and from canyons dominated by willow, mesquite, salt cedar, and mulefat (Bicket 1982); the latter habitat type could be considered desert riparian.

CHIHUAHUAN DESERTSCRUB HABITATS

The Chihuahuan Desert is a high-elevation desert with less of a tropical flavor than the Sonoran or Mohave deserts. Like the Mohave and Sonoran, the Chihuahuan Desert is hot in summer, but its winter temperatures tend to be much colder. Perhaps because of its greater elevation and cold winters, Gila Monsters occur in only a small fraction of the Chihuahuan Desert along its northwestern terminus in southeastern Arizona and southwestern New Mexico (plate 25; figure 6).

A great majority of the soil in the Chihuahuan Desert is derived from limestone parent material, which, in combination with its cool winter temperatures and moderate rainfall (200–305 mm or 8–12 in. per year), contributes to the occurrence of grasses, yuccas, and agaves. In some areas within the Chihuahuan Desert, it is difficult to recognize whether you are in desertscrub or desert grassland. Gila Monsters seem to frequent habitats in which Chihuahuan desertscrub merges with desert grassland along the Gila River and in mountain foothills and canyons on both sides of the New Mexico–Arizona border (plate 25). Some of the best habitat is found along the Gila River in southwestern New Mexico and southeastern Arizona. In this area, Gila Monsters frequent bluffs, rocky slopes, and small, dry canyons. Dominant vegetation consists of creosote bush *(Larrea tridentata)*, catclaw *(Acacia greggii, Mimosa biuncifera)*, snakeweed (*Guitierrezia* sp.), ocotillo *(Fouquieria splendens)*, mesquite *(Prosopis juliflora)*, juniper *(Juniperus monosperma)*, cacti (*Opuntia* spp.), sotol *(Dasilyrion wheeleri)*, and grasses.

WOODLAND

Madrean evergreen woodlands centered in the Sierra Madre of Mexico extend northward into the mountains of southeastern Arizona and southwestern New Mexico. At lower elevations, these woodlands are open and comprise oaks (emory oak, Arizona white oak, and Mexican blue oak are the most common), alligator bark and one-seed junipers, and Mexican pinyon (D. E. Brown 1982). Little is known about specific habitats used by Gila Monsters in madrean evergreen woodlands because they are so rarely observed in that biotic community. Gila Monsters only occasionally visit the woodland in areas where it borders their more preferred habitat type—the semidesert grassland.

An overview of habitat types used by Gila Monsters suggests that they do not prefer truly desertlike biotic communities. They avoid the driest, hottest regions of the southwestern deserts and, in fact, seem to thrive in what many desert ecologists do not consider to be desert communities at all: the thornscrub (which could be argued to include Arizona upland, the most preferred habitat type) and semidesert grassland. Were it not for the occurrence of Gila Monster populations within portions of the Mohave Desert, one might not consider *H. suspectum* to be a desert lizard at all!

MICROHABITAT USE

The habitats occupied by *Heloderma* all provide a suite of resources necessary for survival. What specific features of these habitat types are important to *Heloderma?* Crisscrossing nearly all Gila Monster habitat types are the ever-important drainage channels, or arroyos. Although arroyos are normally dry on the surface, they have much greater belowground water availability than the surrounding upland. Plant communities are often larger in stature and more diverse along arroyos, and soils are usually sandy or gravelly and easily dug into. Along larger arroyos, riparian woodlands may develop as a ribbon of dense vegetation in sharp contrast to the more open surrounding desertscrub. Many animals use the thicker plant cover of arroyos as shelter and as a source of food and nest sites. *Heloderma* often uses arroyos as sites for foraging and shelters.

Some mammals may enhance microhabitat for Gila Monsters by constructing belowground burrows or aboveground middens that ameliorate the often-harsh conditions on the surface. Pack rats (or wood rats) in the genus *Neotoma* build mounds of cactus parts, sticks, and other debris, forming shelters. Many desert reptiles, including rattlesnakes (especially *Crotalus atrox*) and Gila Monsters, take advantage of the moderating effects of pack rat mounds by using them as shelters, and as nest sites (D. F. DeNardo, unpublished data). The more stable soil at the base of many desert shrubs provides suitable conditions for burrow construction by pocket mice, kangaroo rats, and ground squirrels. These burrows are often investigated by foraging Gila Monsters and the larger ones may occasionally be modified and used as refuges. Burrows dug by kit foxes, coyotes, and badgers may also be used as shelters by *Heloderma*. Such burrows and pack rat middens likely are even more important as refuges in barren, open valleys, such as those of the lower Colorado subdivision, where reduced topographical relief provides fewer options for retreat into rocky shelters.

Beaded Lizards use a variety of microhabitats within their dry forest environment. Both tropical dry forest vegetation types—deciduous upland and semideciduous arroyo forest—are visited by Beaded Lizards, but the dense forest of slopes and uplands appears to be used more frequently (Beck and Lowe 1991). Rocky slopes and sandy banks along arroyos are also commonly visited; this occurs especially during the spring nesting season of the Spiny-tailed Iguana (*Ctenosaura pectinata*), whose eggs are exhumed and eaten by foraging Beaded Lizards (see chap. 7). Beaded Lizards also venture into open savannas and cultivated pastures along forest edges, where they occasionally modify mammal burrows for use as shelters. Most ground shelters, however, occur along slopes of small gullies that crisscross the forest (fig. 18). Because these gullies are such a dominant feature of the tropical dry forest landscape, they do not seem to be selected as shelter sites in amounts that are out of proportion to their abundance (Beck and Lowe 1991).

HOME RANGE AND DISPERSION OF SHELTERS

Home range is the area within an organism's habitat through which it moves to fulfill its resource needs, including shelter, energy, water, mates, and nest sites. Home ranges of animals can be represented in many ways. One of the most common is to make a map, connecting points denoting where an individual has been relocated so as to construct the smallest convex polygon that encompasses all observed locations (Jennrich and Turner 1969). If an animal is monitored closely and long enough to accumulate a sufficient number of relocation points, a good map emerges of the various areas within the home range that are used by the individual or population in question.

Based on this method, home range size varies from approximately 12 to 38 hectares (ha) for *H. horridum* and approximately 6 to 147 ha for *H. suspectum* (table 13). At one site in southern Arizona, mean gross home range was 48.1 ha for adult Gila Monsters and 13.4 ha for subadults (Gallardo et al. 2002). In another Arizona study, of relocated Gila Monsters near Phoenix, home range size varied from approximately 6 to 68 ha in lizards that were not relocated to 95 to 190 ha in Gila Monsters that were relocated at least 1 km from their initial site of capture (Sullivan et al. 2004; chap. 9).

Obviously, home range size varies tremendously among individuals and even populations (table 13). There appears to be a modest trend for males to have larger home ranges than females (the two smallest home ranges belong to females), and this trend may become statistically significant during spring and dry summer months (Gallardo et al. 2002) when males are searching for females (chap. 8). No significant difference in home range size between males and females has yet been demonstrated over an entire year (table 13; Sullivan et al. 2004).

Plate 27 shows a home range image comprising shelter sites used by six Gila Monsters monitored for seven years (1992–98) at Redrock, New Mexico (Beck and Jennings 2003). These shelter sites appear not to be randomly dispersed throughout the study site but instead appear clustered in certain areas. Upon noticing this pattern, we wondered whether habitat use by Gila Monsters was influenced by availability of potential shelters. To test this, we set up transects in areas we defined as "high use" (over two Gila Monster visits/ha) and "low use" (<1 visit/ha) and we counted all potential shelters available to Gila Monsters on these transects. We found that Gila Monsters indeed spent far more time in habitats harboring a higher density of available shelters. The high-use areas had, on average, 175 potential shelters per hectare, whereas the low-use areas had only 10/ha (Beck and Jennings 2003). We also found that high-use habitat areas harbored potential shelters that were rockier than those in low-use areas and occurred on slopes oriented more to the south and east. These results suggest that habitats are selected based, in part, on the availability and quality of

TABLE 13

Helodermatid Lizard Home-Range Estimates

LIZARD NO.	SEX	HOME RANGE (HA)	NO. OF SHELTER RELOCATIONS
H. h. horridum, Jalisco (Beck and Lowe 1991)			
1	F	24.0	12
6	M	21.0	38
7	M	39.8	28
10	F	12.0	34
15	M	11.0	14
	Mean	21.6	
H. s. cinctum, Utah (Beck 1990)			
14	M	66.2	41
18	M	32.6	23
20	F	5.6	15
	Mean	34.8	
H. s. cinctum, Nevada (Gienger 2003)			
020	—	85.4	50
040	—	50.9	46
090	—	70.6	24
130	—	18.8	24
170	—	147.4	20
190	—	54.7	28
350	—	21.4	19
	Mean	64.2	
H. s. suspectum, Arizona (Gallardo et al. 2002)			
1	F	25.2	42[a]
2	M	28.7	124
3	M	82.7	89
4	M	55.6	80
6	SA	11.7	73
8	SA	15.0	20
	Mean	36.5	
H. s. suspectum, New Mexico (Beck and Jennings 2003)			
1	M	88.2	46
2	F	40.4	42
4	M	60.0	17
5	M	41.0	36
8	M	65.8	67
9	F	6.2	28
10	F	104.8	38
	Mean	58.1	

NOTE: SA, subadult.

[a] Shelter relocation counts include shelters plus other relocations on surface.

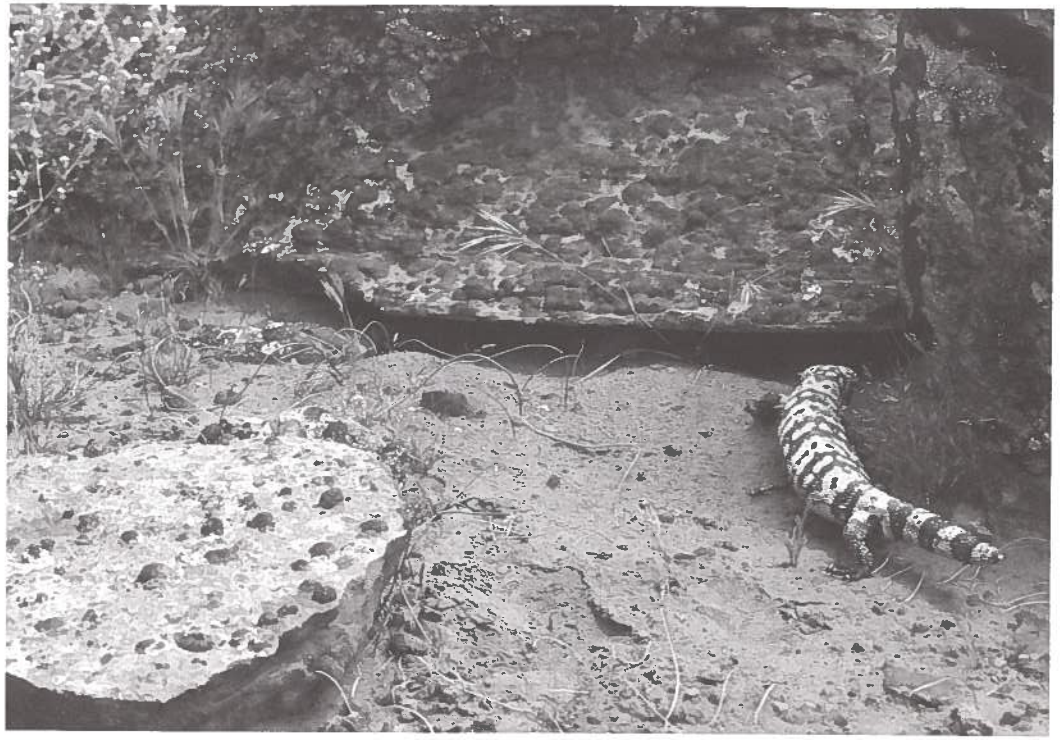


FIGURE 26. Shelters are a vital resource for helodermatid lizards, providing refuge from predators, severe temperatures, and desiccation. Gila Monsters may show strong fidelity to specific shelters.

potential shelters and that shelters may be a potentially limiting resource to Gila Monsters. Because Gila Monsters and Beaded Lizards may spend over 95% of their time resting within shelters, it may be instructive to take a closer look at this important microhabitat feature.

THE ROLE OF SHELTERS

Shelters provide escape from extreme surface temperatures and predators and allow access to favorable thermoregulatory sites, foraging areas, and potential mates (fig. 26). The shelter of a Beaded Lizard or Gila Monster can be a burrow dug by a mammal, tortoise, or Spiny-tailed Iguana; a cavity or crevice on a rocky slope or among boulders; a hollow tree branch or trunk; or a pack rat midden. Gila Monsters and Beaded Lizards generally use preexisting cavities as shelters, although they occasionally modify shelters, especially soil burrows, by digging (Beck 1990; Beck and Lowe 1991; Beck and Jennings 2003; Gienger 2003).

What makes a shelter suitable for use by *Heloderma?* That depends, in part, on the composition of the shelter and the time of year. The structural features of a shelter affect the microenvironment inside it. For example, soil burrows tend to be cooler and retain moisture better than rocky shelters; shelters with entrances oriented toward the south tend to be hotter and drier than those with north-facing entrances. The deeper the shelter, the greater its internal microenvironment is buffered from swings in temperature and humidity that occur on the surface (Beck and Jennings 2003). In addition, shelters with rocky roofs are generally more stable and less susceptible to collapsing.

How do these relationships between shelter structure, microenvironment, and stability influence how shelters are chosen by *Heloderma?* At our New Mexico study site, we addressed this question by comparing traits of shelters observed to be used by radio-equipped Gila Monsters (actual shelters) with nearby potential shelters that, as best we could determine, had not been inhabited by any of the Gila Monsters we were radiotracking (potential shelters). Using such a site/nonsite approach, we found actual shelters to be significantly deeper (mean = 68 cm) than their nearest "potential" shelter (mean = 30 cm). Most interesting was that actual shelters selected during the activity season (April–June) showed a significantly lower vapor pressure deficit than paired potential but unused shelters (fig. 27). Vapor pressure deficit (VPD) is an index of the drying capacity of the air, and it varies with temperature and humidity conditions. This result suggests that vapor pressure is an important factor in shelter selection during late spring and dry early summer, when Gila Monsters show one of their greatest peaks in activity (see below). We detected no differences in temperature between actual and potential shelters, nor did occupancy by a Gila Monster significantly affect the temperature or humidity microenvironment within the shelter (Beck and Jennings 2003).

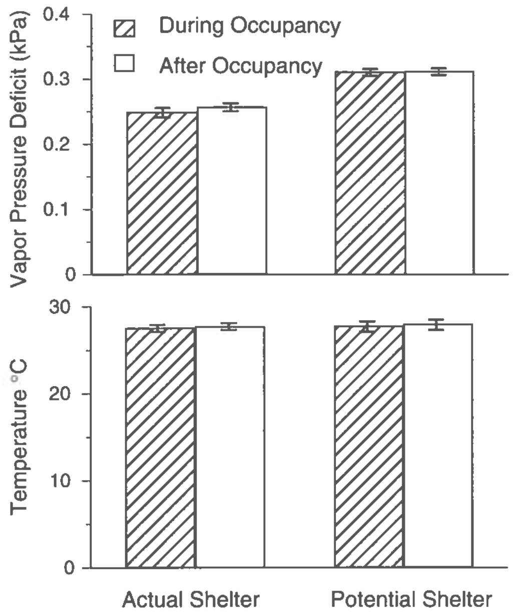


FIGURE 27. Site–nonsite comparison of the microenvironment within Gila Monster shelters at Redrock, NM. Seventeen shelters used by Gila Monsters were paired with similar potential, but uninhabited, shelters and monitored for 48-hour periods (during and after occupancy) during the dry early summer. Vapor pressure deficit, an index of the drying capacity of the air, is an important factor in shelter selection. Values reported are means plus/minus one standard error (horizontal bars). After Beck and Jennings 2003.

How might the extreme seasonal changes that occur in habitats occupied by helodermatid lizards affect their use of shelters? Figure 28 shows how temperature and humidity vary over the course of a year at our New Mexico study site and how these changes naturally result in the five seasons we refer to as winter, spring, dry summer, wet summer, and fall. As these seasons change, so too do the traits of shelters selected by Gila Monsters. During winter, when surface temperatures are frequently below freezing, Gila Monsters select shelters with south-facing entrances on south-facing slopes that are rockier and deeper, and, consequently, warmer than shelters used in other seasons. During dry summer, when surface temperatures are hot, the vapor pressure deficit is high, and desiccation becomes a threat, Gila Monsters select shelters that are more variable in orientation, more soil-like in composition, and, consequently, cooler and more humid than shelters used in other seasons. During spring, when surface conditions are more benign and Gila Monsters are foraging, basking, searching for mates, and pairing within shelters, the shelters tend to be oriented more strongly toward the east, rockier, shallower, and, consequently, more variable in temperature and humidity than other shelter types (Beck and Jennings 2003).

The orientation of the shelter entrance influences thermoregulatory options available to a Gila Monster when it emerges to bask. Both basking behavior (chap. 4) and shelter orientations vary with the seasons. Figure 29 shows how the orientation of shelter entrances changes seasonally. During winter, south-facing entrances provide better opportunities for basking. In spring (March through early May), Gila Monsters show a peak of activity in the morning (see below) and often bask at shelter entrances prior to activity (see fig. 17). A preference for east-facing shelters in spring, therefore, allows more efficient thermoregulation at shelter

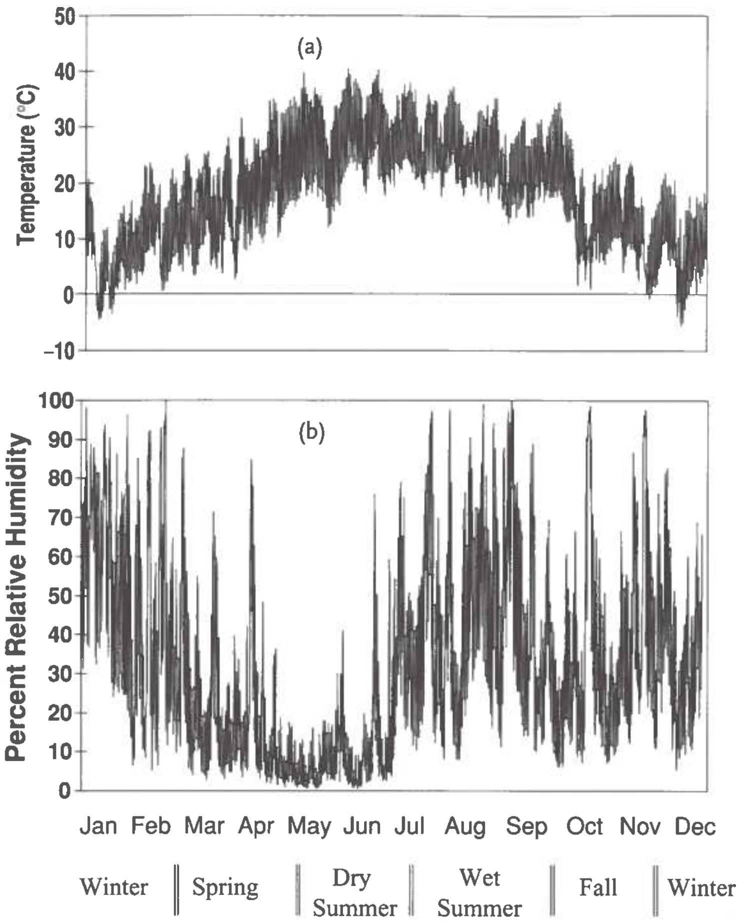


FIGURE 28. Patterns of variation in ambient temperature (A) and humidity (B) over a typical 1-year period on the Redrock, NM, study site. These patterns lead to the five seasons outlined at the bottom.

entrances at a time of year when basking behavior is important.

The amount of time a Gila Monster spends within a particular shelter also changes with the seasons (table 14). During winter, shelters remain constantly occupied for an average of nearly 3 months, whereas during summer, Gila Monsters switch shelters, on average, every 4–5 days. It is not uncommon, however, to observe Gila Monsters remaining within shelters for extended periods even during summer, especially during drought conditions. For example, one female I was radiotracking in New Mexico remained in a dry summer shelter for 40 consecutive days in May and June 1994; and a Utah male remained in a shelter for 13 consecutive weeks in August and September 1983.

For the Beaded Lizard, arroyos, rocky slopes, and the forest floor, including both dense and more open understory vegetation, all provide suitable substrata for shelters (fig. 30). A typical ground shelter is an abandoned burrow with a 15-cm-diameter opening and a tunnel extending inward 1–2 m, situated along a gully bank or slope above a small drainage and often at the base of a tree (fig. 18). *Heloderma horridum* rarely digs its own shelters, unless it is excavating a nest that it later uses as a shelter. The directional exposures of 71 ground shelter entrances I identified in Jalisco were not significantly different from being randomly oriented (Beck and Lowe 1991). Apparently in the more consistently warm (and shady) dry forest environment at lower latitudes, basking behavior is not as common and the directional orientation of the shelter entrance is not as important for thermoregulatory purposes (chap. 4). Lizards inside ground shelters were usually situated about one meter from the entrance. During the surface-active season, Beaded Lizards remained within shelters for an average of 2.3 days (± 1.4, $n = 106$; Beck and Lowe 1991) before moving to another shelter. During winter, Beaded Lizards may remain within winter shelters for weeks at a time (the mean in Jalisco was approximately two weeks before moving to a new shelter). In comparison with the Gila Monster, therefore, Beaded Lizards more frequently switch shelters during winter.

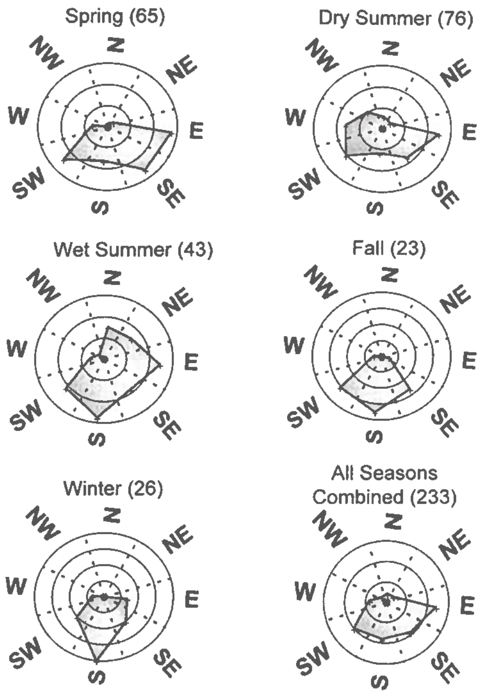


FIGURE 29. Seasonal patterns of Gila Monster shelter entrance orientations, expressed as percentage of sample size falling in each of eight directions. Each concentric circle represents 10% of the sample. Numbers in parentheses are sample sizes. Shelter entrance orientations vary significantly with the seasons ($p < 0.025$; after Beck and Jennings 2003).

Trees are commonly used as shelters by Beaded Lizards, especially during rainy periods. Of 16 tree shelters I identified in Jalisco, 13 were used during or shortly after rain, 11 of which were during the wet season months of July through October (fig. 30). Both hollow branches and trunk sections 2–8 m above ground (mean = approximately 3.5 m) served as tree shelters (Beck and Lowe 1991). Interestingly, during a very heavy rain in September 1988, two *H. horridum* I was radiotracking in Chamela moved into tree shelters as the storm began and remained in those shelters until well after precipitation from the storm had ceased. This behavior suggests that Beaded Lizards may move into trees to avoid flooding during intense storms.

SHELTER FIDELITY

One of the most striking phenomena I've noticed from 20+ years of radiotracking *Heloderma* is their incredible familiarity with the terrain they inhabit. Time and again I am struck by how individuals return season after season, year after year, to the same retreats, some of which are little more than tiny, inconspicuous crevices on a hillside. On a visit to Redrock in May 2002, we stumbled upon No. 9, an individual I began radiotracking 10 years earlier, less than 10 m from her original capture location. I would hazard to speculate that as individuals get older and develop greater familiarity with the microhabitats within their territory, their activity

TABLE 14

Seasonal Patterns of Shelter Occupancy by Gila Monsters in Southwestern New Mexico between December 1992 and June 1994

SEASON	[1] SPRING	[1] DRY SUMMER	[1] WET SUMMER	[2] FALL	[3] WINTER
(*n*)	(48)	(43)	(24)	(22)	(9)
No. of days in same shelter	5.1 ± 1.00	4.5 ± 1.08	4.2 ± 0.77	13.6 ± 2.46	88.7 ± 1.21

NOTE: Values shown are means followed by ± one standard error; those with the same superscript number did not differ significantly (from Beck and Jennings 2003).
n = no. of shelters

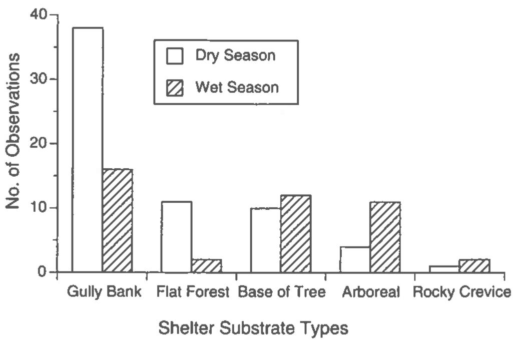


FIGURE 30. Shelter types used by *H. horridum* in a tropical dry forest in Chamela, Jalisco. During the rainy season, Beaded Lizards more commonly used trees as shelters and more frequently avoided gully banks (after Beck and Lowe 1991).

range actually shrinks as they develop a preferred set of familiar retreats.

Just how faithfully do Gila Monsters revisit previously reused shelters? From our radiotracking studies in New Mexico, we found that nearly half of the shelters visited by Gila Monsters had been used before. However, that is probably an underestimate of actual refuge-site fidelity because the longer we tracked lizards the more we observed them returning to previous retreat sites (Beck and Jennings 2003). At Redrock, New Mexico, Gila Monsters show the greatest fidelity (73%) to retreats at which they overwinter, a result that suggests they are less willing to "experiment" with such shelters, which serve as important refuges from cold and predators for over 30% of the year. Some shelters that were used as winter refugia, however, were also reused during dry summer at Redrock. In southern Arizona, Brent Martin has recaptured the same Gila Monster basking outside its winter retreat for up to 17 years running (see chap. 6)!

What is so special about reused shelters? At Redrock, reused shelters tend to have rockier roofs than those of other shelters, a result probably attributable to their greater durability (shelters with soil roofs are vulnerable to collapse). Aside from rockiness, however, reused shelters do not differ structurally from shelters not observed to be reused. In terms of time spent within shelters, however, Gila Monsters show tremendous fidelity to familiar sites, spending over five times longer in reused shelters as in shelters we observed to be used only once (see fig. 31). Familiarity with a particular shelter may thus be another important cue used in refuge-site selection by Gila Monsters, a trait they may also share with other reptiles. For example, Sleepy Lizards *(Tiliqua rugosa)* use specific visual cues to recognize shelters. They prefer familiar cues over novel ones, which may play a role in the fidelity they show to particular habitat areas within their home ranges (Zuri and Bull 2000).

Shelter fidelity has an important social context. Of 93 shelters that were reused by Gila Monsters at Redrock, 46% were used by more than one individual (social shelters). Of these 43 social shelters, 54% were used by two or more lizards concurrently, usually during April through June when mating occurs and when we observed males and females together within shelters (see chap. 8). These sites play an important role in the social structure of the population. Males fight in spring for access to such shelters and mating likely takes place in them during April–June (chap. 8). Moreover, male Gila Monsters may deposit cloacal chemical cues at the entrance to social shelters during the breeding season (Beck 1990; chap. 8). At Redrock, social shelters showed differences from individual shelters in their spatial arrangement.

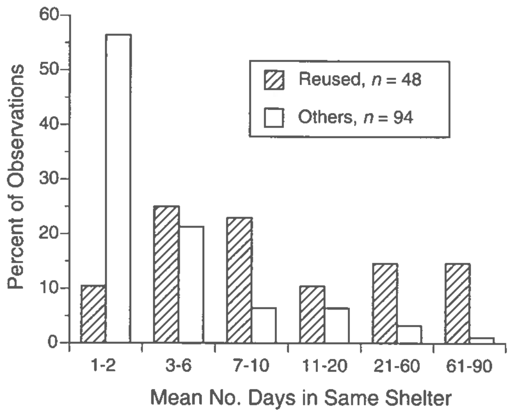


FIGURE 31. Shelter "residence times" at the Redrock study site. Gila Monsters spent over five times as much time in reused shelters as in those observed to be used only once (from Beck and Jennings 2003).

A majority of social shelters was located near the core of our study site where lizard home ranges overlap (plate 27), whereas a majority of shelters reused by individual lizards was composed of overwintering refugia located near the edges of home ranges.

Fidelity to established retreat sites is not unique to Gila Monsters. Many other reptiles, including snakes (Reinert and Zappalorti 1988; Ciofi and Chelazzi 1994; Webb and Shine 1997), lizards (Norris 1953), and tortoises (Burge 1977; Bulova 1994; B.E. Martin 1995) have shown strong fidelity to specific retreat sites. Desert rodents construct elaborate burrow systems that provide protection from predators and harsh surface conditions and to which they show strong fidelity (Schmidt-Nielsen 1964; Murie and Michener 1984; Burns et al. 1989; Goyol and Ghosh 1993). Desert macroinvertebrates, including burrowing spiders (Humphreys 1978; Marshall 1997), scorpions (Polis et al. 1986), and beetles (Rasa 1995) may also show fidelity to retreat sites. Such species are closely dependent on suitable refugia, and their patterns of distribution and abundance may be related to the availability of suitable substrate in which burrows can occur (Feldhamer 1979; Kinlaw 1999).

In summary, habitat use by helodermatid lizards is closely tied to shelters, which are crucial to their survival in strongly seasonal arid environments. Shelters provide stable microenvironments, access to mates, and refuge from harsh conditions and predators on the surface. Shelters, and the habitats where they occur, are not chosen at random. Helodermatid lizards select shelters based on specific attributes, alter their choice of shelters as conditions change seasonally, and develop preferred retreat sites to which they return year after year. Such prudent use of habitat also requires careful timing of activity.

ACTIVITY PATTERNS

The primary objective of surface activity by Gila Monsters and Beaded Lizards is to find food, mates, or appropriate shelters. Supply and demand for these resources obviously change with the seasons. Finding resources may be more challenging, and require more searching, in some years (and some locations) than in others. Many animals cope with strongly seasonal environments by becoming dormant during the dry season or by migrating to less harsh environments (Ceballos 1995). The strong seasonality of habitats occupied by *Heloderma* greatly affects the timing and intensity of activity. Thus one cannot consider activity without putting it in a seasonal context.

Beaded Lizards are most easily encountered active along roads and trails just after the summer rainy season begins in their tropical dry forest habitats, usually in July. This pattern suggests that Beaded Lizards show their greatest activity during the rainy season. When I began radiotracking Beaded Lizards, I was, therefore, surprised to find a significant peak of activity in May, among the driest periods of the year in the tropical dry forest. In terms of total time spent on the surface and distances traveled per activity bout, Beaded Lizards at my study site in Jalisco covered more ground in May than during the wet season months of July or September (fig. 32). Animals were most frequently sighted in early May, although considerable activity continued throughout June and July, gradually decreasing in September and October. Lizards were frequently encountered on the surface after rains, especially at the onset of the rainy season in July. During winter, activity decreased considerably, although some surface activity likely occurs during every month of the year (Beck and Lowe 1991; see fig. 32).

ACTIVITY BOUTS AND SPRINT SPEED

During their aboveground travels, Beaded Lizards often follow the slopes and bottoms of the numerous small drainages that cut through upland forest, covering distances ranging from 15 m to over 1 km (Beck and Lowe 1991). They move slowly and deliberately, carefully investigating the surroundings with their sensitive forked tongues (see chap. 4). The mean of 116 Beaded Lizard forays I observed in Jalisco was

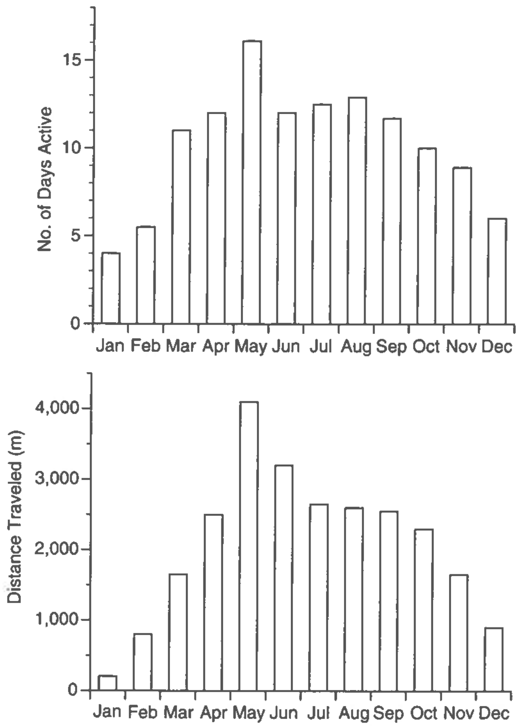


FIGURE 32. Estimates of Beaded Lizard activity. Values shown are means derived from radiotracking six Beaded Lizards in a tropical dry forest in Chamela, Jalisco, Mexico (modified from Beck and Lowe 1991).

236 ± 153 m. Their rate of travel varied from 42 to 420 m/hour with a mean of about 210 m/hour (3.5 m/minute), resulting in a duration of approximately 67 minutes for a typical foray.

Like Beaded Lizards, aboveground travels taken by Gila Monsters range from short trips of a few meters around shelter entrances to journeys of over a kilometer. Longer trips seem to occur more frequently soon after Gila Monsters leave their overwintering shelters and actively forage and seek mates. Some individuals also partake in extended journeys in late summer or early fall as they make their way back to overwintering sites. Other lizards, however, may show little spatial separation between their summer and winter territories and therefore less seasonal variation in the length of their forays. During a "typical" aboveground activity bout, a Gila Monster will cover approximately 250 meters as it carefully investigates its surroundings with its forked tongue (Beck 1990; Beck and Lowe 1991; chap. 7). The mean foraging pace of a Gila Monster is around 250 m/hour (Beck 1990). Of course, speed, duration, and extent of these forays vary considerably. For example, Beaded Lizards may emerge from shelters more frequently during the rainy months of July and August but do not necessarily travel as much (per activity bout) as they do during the dry season. Moreover, some individuals tend to be more active overall, traveling much farther—and more frequently—than others. Activity may also vary from year to year and from location to location (Beck and Lowe 1991).

Nevertheless, the mean distance and duration of aboveground activity bouts appear similar for Gila Monsters and Beaded Lizards. Neither species is particularly speedy during these above-ground forays, even when fleeing from potential predators. The fastest Beaded Lizard we ever recorded ran at 2.3 km/hour (or 1.4 miles/hour; Beck et al. 1995); the fastest Gila Monster was a bit slower at 1.9 km/hour (or just over 1 mile/hour). Their average top speed of 1.7 km/hour (about 1 mile/hour) puts them near the bottom of the pack in lizard sprint speed performance, especially when compared with some desert lizards that reach sprint speeds of over 25 km/hour (or 15 miles/hour, which approaches human top speed; Garland 1984; Beck et al. 1995).

What they lack in speed, however, helodermatid lizards seem to make up for in determination. As they walk, Gila Monsters and Beaded Lizards show a unique, deliberate undulating gait, alternately swinging their front, then hindquarters, from side to side, "as if the front and back halves haven't agreed on the same direction" (Malusa 1993), a motion I refer to as the "*Heloderma* shuffle." They are also quite adept at walking backwards, especially when threatened. A foraging Gila Monster will frequently stop, turn its head—almost as if listening—then continue on its way. It is likely that Gila Monsters use a relatively keen sense of hearing to help locate cottontail nests (where the juveniles within often emit muffled grunts and squeaks), although this idea has not been carefully tested. Gila Monsters and Beaded Lizards active on the surface certainly seem to be sensitive to sounds made by potential predators, such as a human investigator. When radiotracking Beaded Lizards and Gila Monsters, I have noticed the lizards abruptly stop, even turn to flee, at my making the slightest noise such as crushing a leaf or twig on the ground. Upon approaching a Beaded Lizard that had not yet detected me, I once stood quietly and completely motionless while I watched the lizard walk up to investigate my pant leg, then crawl over my boot on its way to the next object of interest.

Both species are good climbers. Gila Monsters will, on occasion, deliberately and skillfully climb into trees, although they appear to descend with some difficulty. Gila Monsters have been observed up to 2.5 m above ground in desert willow (*Chilopsis linearis;* Cross and Rand 1979). Many potential prey (e.g., doves) nest in trees and subtrees (small trees, such as paloverde, white thorn acacia, mesquite, and ironwood), so it should not be surprising that Gila Monsters climb after them. Gila Monsters are also skillful at scaling arroyo banks and rocky slopes. I have watched individuals in rocky habitats of the Mohave Desert scale very steep sandstone cliffs. Beaded Lizards are even more adept at climbing than are Gila Monsters. Their proportionately longer bodies and semiprehensile tails enable them to ascend and descend trees with relative ease. Beaded Lizards commonly climb up to 5–7 m into trees where they may forage for nests and use hollow trunks and branches as shelters (plate 28; Beck and Lowe 1991; Campbell and Lamar 2004).

GILA MONSTER ACTIVITY: SEASONAL PATTERNS

In southern Arizona, Gila Monsters commonly emerge during January and February to bask at shelter entrances and will even forage and feed during the winter months (B.E. Martin, pers. comm.; chap. 7). As with Beaded Lizards, Gila Monsters show a peak in activity in spring, especially during May (fig. 33). This pattern holds for both the Sonoran and the Chihuahuan desert regions, which receive significant summer rain, and for sites in the Mohave Desert that are more strongly influenced by winter precipitation.

After the May activity peak, however, activity appears to differ markedly between Mohave Desert populations (dominated by a winter rainfall regime) and Sonoran/Chihuahuan desert populations that are influenced by summer rains. In the Mohave Desert, activity may continue more strongly through June whereas in the Sonoran Desert, activity shows a notable decline at this hottest, driest time of the year. In Nevada, activity was greatest from late May through June but declined sharply in August to about half that of June and only one-third that of May (Gienger 2003). In Utah, 64% of activity occurred from late April to early July (Beck 1990). In a Mohave Desert population in northwestern Arizona, Jones (1983) noted a marked decrease in activity by *H. suspectum* in June and July in comparison with April and May.

A different picture emerges in habitats dominated by summer rainfall. As summer monsoons arrive at Sonoran and Chihuahuan desert habitats in late July and August, Gila Monster activity also picks up, especially in Arizona upland habitats of southern Arizona. Second only to the spring months of April and May, August shows the greatest number of observations of Gila Monster activity (fig. 33). In a population monitored with radiotelemetry in southern Arizona, Gila Monsters were active on 80% of the days they were monitored during the late July–August monsoon season (Mattlin et al. 2003). As monsoonal rains declined in September, activity decreased abruptly to under 20% of the days lizards were monitored (Mattlin et al. 2003). In contrast, Gila Monsters in the Mohave Desert, where summer rain is much more rare, do not show such a strong late summer surge in activity (see fig. 33). Regardless of location, however, *H. suspectum* becomes less active on the surface with very hot and dry summer temperatures and may remain within shelters for weeks at a time (Lowe et al. 1986; Beck 1990). All populations show a marked decrease

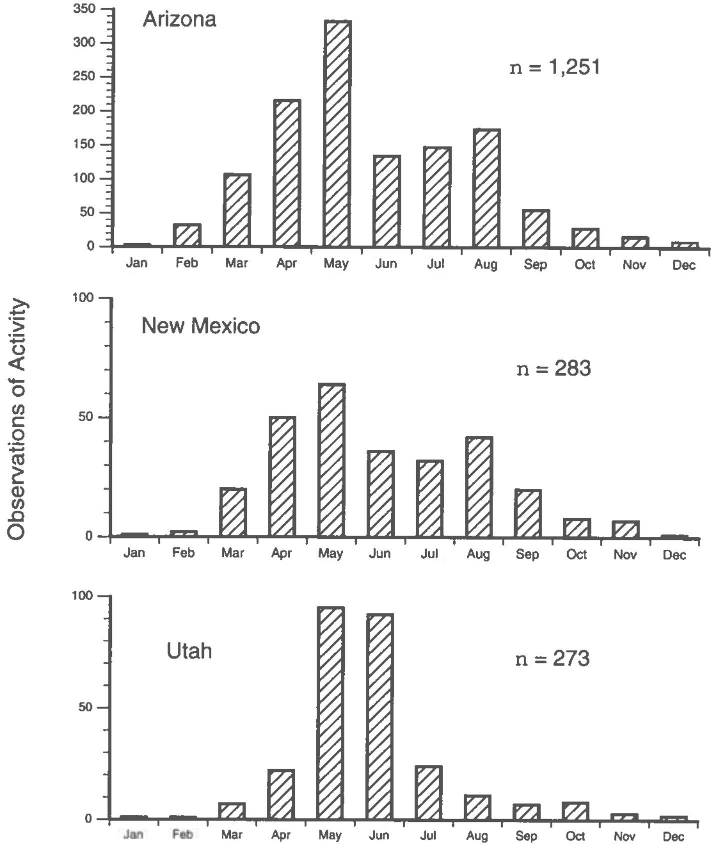


FIGURE 33. Monthly patterns of Gila Monster activity based on the timing of encounters of surface-active lizards in the field. Activity peaks in May, but in the Sonoran and Chihuahuan desert regions of Arizona and New Mexico a second pulse in activity follows the summer monsoon season.

in activity during winter, and most individuals remain within shelters for 2.5 to 4 months during that time.

Interestingly, monthly timing of the activity of *H. suspectum* may vary with age. Newly hatched Gila Monsters are encountered from May through August. Larger, but still subadult, individuals show a broader window of activity, peaking in July. A late spring (i.e., April/May) peak in activity is not evident until individuals approach the larger size classes, over 255-mm SVL (fig. 34).

In some populations, activity increases during the summer monsoons, but throughout their range, adults of both species of *Heloderma* seem to show a peak in activity near the end of the dry season, a time of year when the risk of desiccation is very great. This pattern seems paradoxical given the high water loss rates of helodermatid lizards (chap. 4). As spring approaches throughout the range of the Gila Monster, so too does the availability of potential prey. Several prey species show a reproductive pulse in March–May (chap. 7). Moreover, sperm production in Gila Monsters occurs from April to June (peaking in May), a time when females are also reproductively receptive and when males and females commonly pair inside shelters (chap. 8). Prey availability and reproductive behaviors may thus explain the peak in activity shown by Gila Monsters in spring. The late-dry-season pulse in activity by *H. horridum* is not as easily explained as for *H. suspectum*. At Chamela, it may, in part, be a response to the explosive reproductive output shown by Spiny-tailed Iguanas, which nest during the late dry season.

Given the variability in the timing of seasonal activity, one might also expect seasonal variation in the time of day that activity occurs. A perennial debate has centered on whether helodermatid lizards are diurnal or nocturnal.

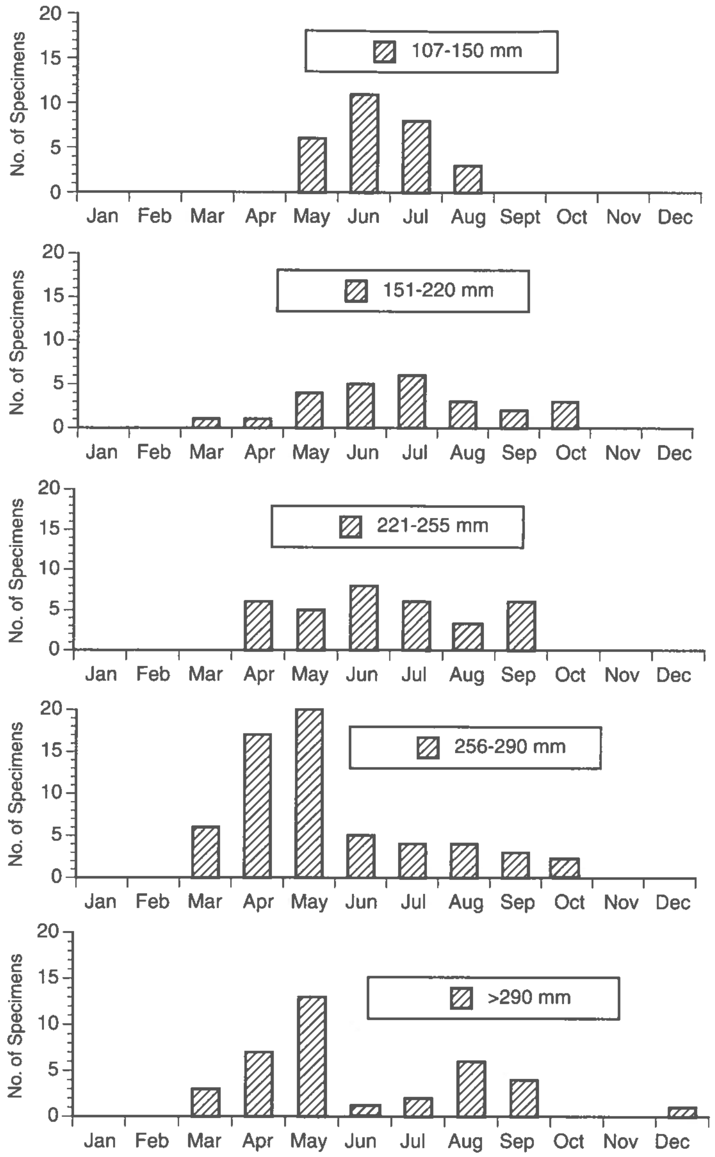


FIGURE 34. Seasonal activity patterns of Gila Monsters in relation to the size classes described in chapter 6 (and based on collecting and analyzing information from 186 specimens in the University of Arizona herpetology collection). Note the relatively narrow period (May–July) shown by hatchling-sized lizards (top) and the pulse of activity in May shown by larger adults.

The appropriate answer is yes. They are active at any time of day or night, depending on surface conditions, which change markedly throughout the year. This simple pattern has not always been obvious to me. The following anecdote provides an example.

A GILA MONSTER IN MY SLEEPING BAG

Late in June 1986, my brother and I left Tucson for a road trip to Jalisco, Mexico. I was a young graduate student at the University of Arizona, eager to begin the first intensive field study on *H. horridum*. I had all my telemetry gear, letters of permission, a small grant from the American Museum of Natural History, and 4 years of field experience—and biases—with Gila Monsters under my belt. One of the biases I had developed was that Gila Monsters were strictly diurnal. The vast majority of Gila Monster activity I had observed in the Mohave Desert of Utah took place during the day, especially in the morning (Beck 1990). I had yet to learn about activity patterns of Gila Monsters in the heart of the lower, hotter Sonoran Desert.

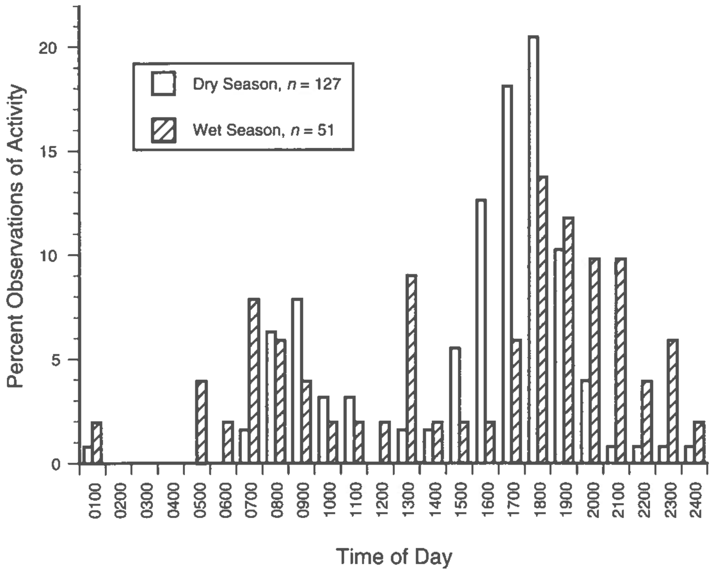


FIGURE 35. Timing of activity of *H. horridum* in Jalisco, Mexico, expressed as the percentage of total observations. Wet season includes July through October. Note that the bimodal activity pattern is more separated during the wet season (after Beck and Lowe 1991).

We found a quiet spot in the desert north of Guaymas, Sonora, to camp our first night. It was still very hot as we bedded down just past dusk, so I pulled my sleeping bag only up to my waist and, despite the heat, it didn't take long for me to drift off to sleep. At 10 minutes past midnight (according to my field notes), I was dreaming. It was a fairly typical dream for a herpetologist. I had just found a beautiful, large Green Iguana *(Iguana iguana)* and was picking it up, holding it with one hand carefully supporting its body and the other grasping it behind the head to avoid being bitten. During this dream, I began to incorporate the sounds and sensations of the surrounding desert and felt something pawing at my sleeping bag. I awoke and realized I was holding something. It took me a second to take it in, but there in my hands was a large adult Gila Monster. I was holding it gently, but snugly, supporting its body with my left hand and grasping its neck with my right hand to avoid being bitten (just as I would normally do). A Gila Monster had crawled into my bedding, and I had naturally picked it up in my sleep! I sat up and stared at the lizard, trying to disentangle dream and reality. Was I really awake, or was this still part of my dream? I called out excitedly to my brother: Jon, a Gila Monster! A @#$%*!! Gila Monster! I can't believe it, Jon, a Gila Monster! A @#$%*!! Gila Monster! Shaken from slumber, my brother exclaimed: "Shut up and go back to sleep, you're just dreaming." But I continued to rant until we both got up and took in this amazing event.

Even though trained as a scientist, I knew this had to be some kind of a sign. Gila Monsters are rarely encountered in the wild, even by experienced field biologists. There I was on my first trip to study *H. horridum*, and an individual of its sister species had crawled into my sleeping bag! And I had thought they were not even supposed to be nocturnal. I concluded that I was blessed with extraordinarily good luck and that my fieldwork in Jalisco would be productive beyond expectations. Two days later, after a 1,300-mile drive, we arrived at the field station in Chamela. I took my brother to the nearest airport, and he flew back home as I began my fieldwork. Two weeks of intensive searching for *Heloderma* passed, but I saw no Beaded Lizards. I contracted salmonella and amoebic dysentery (at the same time) and spent two days in a hospital in Manzanillo. Still no Beaded Lizards. I returned to searching for Beaded Lizards (several pounds lighter) just as the summer rains began falling. Finally, after three weeks of intensive searching, and one month in the field, I encountered my first Beaded Lizard in the Chamela forest and thus began radiotracking these elusive creatures. Finding that first Beaded Lizard turned out to be quite the opposite of having a Gila Monster crawl into my sleeping bag.

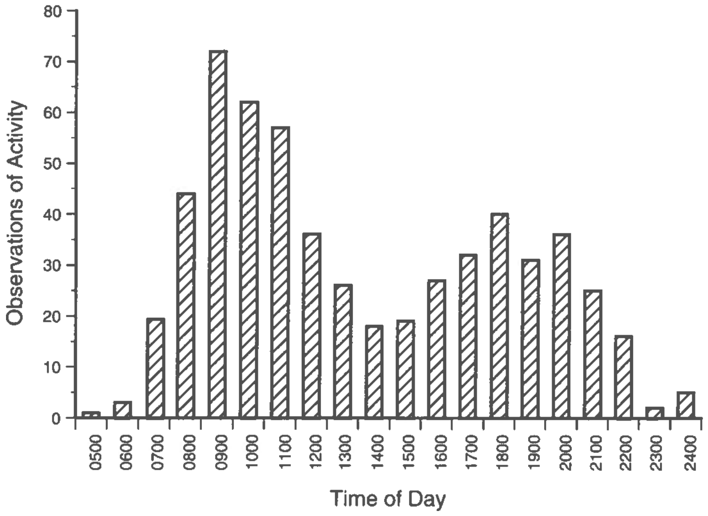


FIGURE 36. Timing of Gila Monster activity in Arizona and New Mexico for the entire year based on radiotelemetry and field surveys (*n* = 571). Data from B. Martin, C. Lowe, R. Repp, B. Sullivan, and D. Beck (unpublished). Data were not corrected for search effort, and, therefore, nocturnal activity is likely underestimated, especially during the hot summer months.

Biases are built on overinterpretations of our experience. Early field guides described Gila Monsters as nocturnal because the first specimens were collected in the Sonoran Desert by researchers searching primarily during summer nights, when considerable nocturnal activity occurs. I had developed my own bias because my early experience told me that most activity in Utah occurred during the day. It turns out that activity times depend on both the locality and the time of year. I had been fooled into thinking I really knew the patterns when I had witnessed only a fragment of the big picture. If not outright dangerous, a little knowledge can certainly be misleading.

TIMING OF ACTIVITY

As the above digression implies, the timing of activity by helodermatid lizards varies seasonally and geographically. In Chamela, Jalisco, *H. horridum* shows a peak in activity in the late afternoon and early evening between 1600 and 2000 hours, with a smaller morning peak between 0700 and 1000 hours (fig. 35). During the rainy season, these two activity peaks are more separated than during the dry season: Beaded Lizards emerge earlier in the morning and later in the early evening (fig. 35). More nocturnal activity in Jalisco occurs during rainy periods. In Chiapas, active *H. h. alvarezi* are more commonly encountered toward dusk and shortly thereafter (less so in the morning); during rain they may emerge from burrows earlier in the day (Álvarez del Toro 1982).

The timing of activity by Gila Monsters is summarized in figures 36 and 37. Throughout much of the year, Gila Monsters show an activity peak in the morning. During fall and winter, this peak occurs late in the morning (between 1000 and 1200 hours) and during spring, it occurs during mid-morning, between 0900 and 1100. As summer temperatures increase during dry summer (mid-May to early July), the morning activity peak is shifted earlier and an evening/nocturnal activity pattern emerges. This bimodal pattern in timing of activity continues through the summer monsoon season, when considerable nocturnal activity also takes place in the Sonoran Desert. During the hottest periods, nocturnal activity may be the norm for some populations, with diurnal activity occurring more commonly on cooler, overcast days.

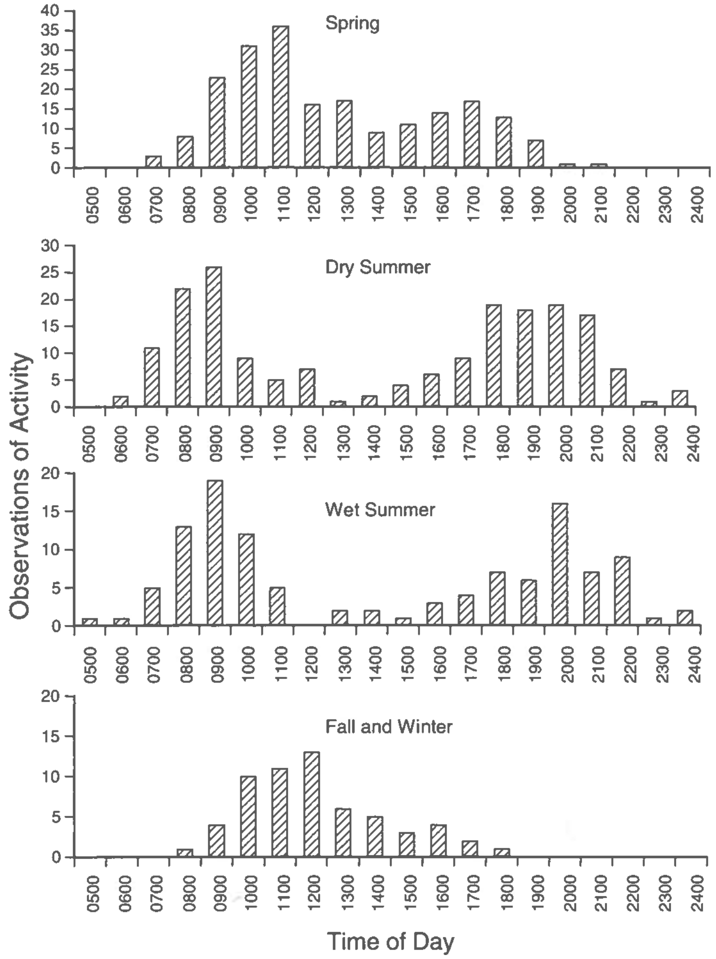


FIGURE 37. Seasonal influences on the timing of Gila Monster activity in southern Arizona and New Mexico ($n = 571$). A bimodal pattern becomes more pronounced as summer progresses. Summer nocturnal activity may be underrepresented because of sampling bias (see text). Data from B. Martin, C. Lowe, R. Repp, B. Sullivan, and D. Beck (unpublished).

Accurately estimating the timing of lizard activity is difficult. Records of activity may be biased by the particular times at which human observers are active gathering data or searching for lizards. For example, observations of the occurrence of *Heloderma* activity between the hours of midnight and 5:00 a.m. are rare; but is this because *Heloderma* are not active at these times or because most field biologists are sleeping and, therefore, less often sampling during the wee hours of the morning? I tried to at least partially correct for such biases in my radiotelemetry studies in Jalisco, New Mexico, and Utah by selecting specific sampling periods that captured all possible hours. Based on this even sampling method, I did not find that I had missed any significant nocturnal activity.

However, in Arizona upland habitats of *H. suspectum*, researchers using telemetry and implantable dataloggers are seeing far more nocturnal activity, especially during the months of July and August, than typically observed by conventional methods of searching roads (D. F. DeNardo, pers. comm.; G. Shuett and R. Repp, pers. comm.). In Arizona upland habitats in the heart of the Sonoran Desert, nocturnal activity appears to be the norm during the summer monsoon season of July and August. Similarly, in the Mohave Desert of Nevada, Gienger (2003) observed an abrupt shift from strictly diurnal activity in May to predominantly nocturnal activity (70% of observations) in July; Crowther (1993) observed considerable activity during warm summer evenings in southwestern Utah.

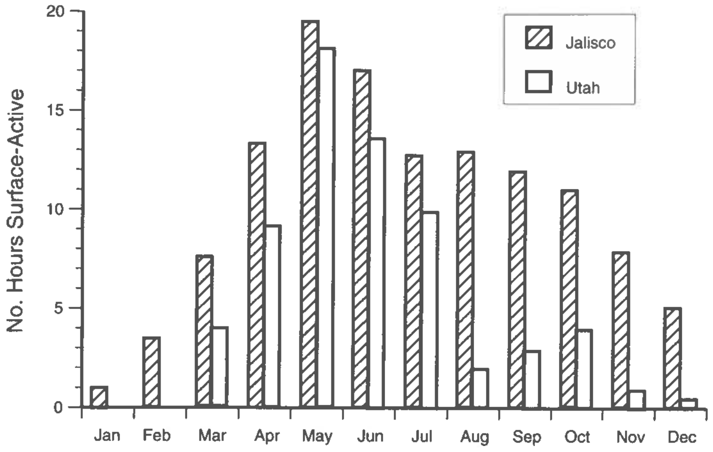


FIGURE 38. Estimates of hours spent active (modified from Beck 1990 and Beck and Lowe 1991) of *H. horridum horridum* at Chamela, Jalisco, and *H. suspectum cinctum* in southwestern Utah.

AMOUNT OF ACTIVITY

From estimates of how frequently they are active on the surface, and the duration of their activity bouts, we can speculate about just how much time Beaded Lizards and Gila Monsters devote to surface activity, and how much time they remain largely inactive in or near shelters. Figure 38 shows an estimate, based on my studies using radiotelemetry, of the mean number of hours per month that some helodermatid lizards are active on the surface. This pattern mirrors that shown in the other activity figures: activity peaks in spring and gradually decreases during summer and winter, depending on latitude. In the Mohave Desert of southwestern Utah (under a winter-rainfall–dominated regime), Gila Monsters only spend about 65 hours per year active on the surface, the vast majority of which takes place from mid-April to mid-July. In the Sonoran and Chihuahuan desert region of southern Arizona and southwestern New Mexico, the activity season begins earlier (in March) and extends throughout the summer monsoons in July, August, and September (see fig. 33). Gila Monsters show greater annual surface activity in these habitats than they do in the Mohave Desert.

Still further south, in Jalisco, Mexico, we find *H. horridum* to be active over an even greater period of the year, traveling approximately 25 km in 121 hours of annual surface activity (Beck and Lowe 1991; figs. 32 and 38).

During September and October, *H. horridum* travels over 10 times as far as a typical *H. suspectum* in southwestern Utah at the northern extreme of the family distribution. Potential prey biomass and species diversity in tropical dry forest habitats are considerably higher than in semidesert habitats of *H. suspectum* to the north. Suitable prey species may be more abundant for *H. horridum* during late summer and fall, a time when *H. suspectum* exhibits reduced activity. In addition, during September through December, Beaded Lizards search for mates, engage in combat and courtship, and lay eggs (chap. 8). These reproductive behaviors may contribute to the extended activity season of *H. horridum* (see also chaps. 4 and 7). Although *H. horridum* in Jalisco invests about twice the time in surface activity as the northernmost populations of the Gila Monster, its overall investment in activity is still low. During May, the month with peak activity, the Beaded Lizards I radiotracked in Jalisco traveled an average of 4.1 km over 19.6 hours of surface activity (Beck and Lowe 1991). The remainder of their time—over 95% of daylight hours—was spent in shelters.

Previous studies of Gila Monsters in Arizona have observed similar low levels of activity (Porzer 1981). Lowe et al. (1986) gave an estimate of a maximum of 190 hours per year spent in surface activity by Gila Monsters in Arizona. More recent work, however, suggests some populations show much greater levels of activity than others. Using radiotelemetry in Nevada, Gienger (2003) found that Gila Monsters traveled over twice as far per activity bout as did those in Utah (Beck 1990). In the Sonoran Desert Arizona upland habitats in southern Arizona, D.F. DeNardo (and students), R. Repp, and G. Schuett are observing an activity surge by Gila Monsters during the summer monsoon. Estimates as high as 500–670 hours/year have been derived from one population (D.F. DeNardo, pers. comm.). Even the highest estimates of 670 hours of activity per year leave 8,090 hours—or over 92% of the year—spent resting in shelters.

CONCLUSIONS

An analysis of habitat use and activity patterns of helodermatid lizards helps us to resolve the paradox of why a lizard with a low temperature tolerance and a leaky skin manages to show an activity peak at the hottest, driest time of year. Their keys to maintaining homeostasis are to choose appropriate shelters and to pass the time protected from the elements (and from predators) within these retreats. Given the relatively small amount of time that helodermatid lizards spend active on the surface and, conversely, the considerable time (>92%) spent within shelters, it might make more sense to talk about patterns of *inactivity* in helodermatid lizards. Although activity is obviously very important for finding food, water, mates, and shelters, the importance of inactivity is often ignored and not very well understood. Inactivity is a hallmark of helodermatid lizards and, because of energy and water considerations (see chap. 4), is also one of their "secrets" to surviving in a highly variable, low-productivity environment.

Although helodermatid lizards inhabit highly variable environments, this need not imply that such biomes are particularly harsh to individual lizards, any more than one would consider their low temperature tolerance and leaky skins "maladaptive." There may be "good" years and "bad" years, in terms of resource availability, but as we have already seen, helodermatid lizards are well adapted to tolerating swings in resource availability. A still greater appreciation of their ability to thrive in variable environments comes from considering the population ecology of helodermatid lizards.

CHAPTER 6

Population Ecology

Daniel D. Beck, Brent E. Martin, and Charles H. Lowe

A POPULATION IS A GROUP of individuals within a single species that inhabits a particular region. Where one population ends and another begins is usually impossible to identify because such groups normally form a continuum across loosely connected (and poorly understood) microhabitats. The boundaries of a population are often defined by the investigator and may be necessarily arbitrary. We might speak of the Sonoran Desert population of Gila Monsters as accurately as we would a more restricted population within a particular desert valley. Populations show particular traits, or emergent properties, that are not present at lower levels of biological organization. Thus we speak of the sex ratio of a population as well as its density, structure, and dynamics. The characteristics of a population are determined by the rate at which its individuals grow to reproduce, the number of offspring produced (fecundity), how long individuals live (longevity), the rate at which they die (mortality), and how frequently members leave (emigration) or new individuals join the population (immigration). Most of these characteristics are difficult to quantify and, therefore, remain largely unknown for helodermatid lizards. Knowing these statistics is very important, however, if we are to understand how populations change over time and how they may be affected by predators or disease, environmental change, and the ever-present onslaught of human population growth and expansion.

In this chapter, we address these population characteristics in helodermatid lizards. We present a summary of our own data, and those of our colleagues, that will help form a foundation for understanding the population ecology of these fascinating lizards.

BODY SIZE

Body size affects almost all traits of an organism, from its metabolic rate to its life span (see Calder 1984; Schmidt-Nielson 1983). Helodermatid lizards span a great range in size from hatchling Gila Monsters, barely 16 cm long, to large, adult Beaded Lizards, approaching 1 m in length. Upon hatching, Gila Monsters emerge with a snout-to-vent length (SVL) of approximately 110 mm (160 mm including the tail). Most adult Gila Monsters fall in the range of 275–335 mm in SVL. Any Gila Monster over 350 mm in SVL or 500 mm in total length may be considered quite large. The largest verified wild Gila Monster on record was brought to the Adobe Mountain Wildlife Rehabilitation Center in Mesa, Arizona, in 1990 and measured

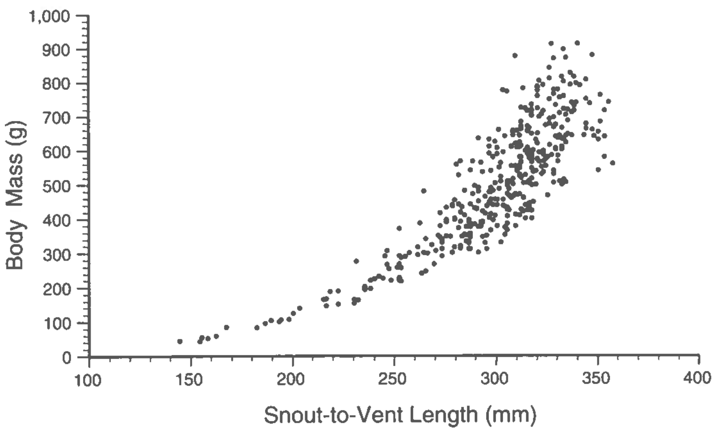


FIGURE 39. Relationship between SVL and mass in noncaptive *H. suspectum*. A greater dispersion of values among larger individuals represents the huge variation in body mass that is related to energy storage.

22.5 in. long, or 570 mm (D.E. Brown and Carmony 1991). The largest Gila Monster we've encountered in Utah was a female measuring 529 mm, with a SVL of 360 mm. The largest Gila Monster from New Mexico, an old male, measured 362 mm in SVL and 514 mm in total length. Despite the statement in popular literature that the Gila Monster reaches 24 in. in length (609 mm), no such animal has been documented. Apparently, adding those last 1.5 in. (49 mm) in length is no small task!

There are colorful stories, however, of Gila Monsters far larger. Perhaps the most preposterous, first printed in the *Arizona Sentinel* (Yuma) on September 15, 1883, is that of two prospectors, Dan Conner and Pilgrim, who claimed to have encountered a 300-lb Gila Monster in the Castle Dome Mountains of Arizona. The monster was so large that the men tried to secure it with cords, but when they returned with still larger ropes to bind their catch, the lizard had broken free and escaped. Connor swore the story was true and even offered to make an affidavit before a notary. An affidavit never materialized, however, nor was this record ever published in a peer-reviewed journal.

In the wild, Gila Monsters seldom reach a body mass of over 1 kg. The heaviest lizards we've recorded in the field are a 936-g Arizona male, an 880-g Utah male, and an 870-g New Mexico male. Although there is generally a strong correlation between SVL and mass (fig. 39), the body mass of individual lizards may vary considerably over relatively brief periods (i.e., months). We've seen Gila Monsters gain nearly 200 grams after a single large meal of cottontail rabbits and lose 160 grams after laying eggs. An adult Beaded Lizard at Chamela showed a 30% weight gain between August and the following May; another individual increased 6.3% in body mass from water uptake after a small rainstorm near the end of the dry season (Beck and Lowe 1991).

Beaded Lizards hatch with a SVL of approximately 120 mm and a total length of approximately 200 mm (Ramírez-Bautista 1994). In nature, adult *Heloderma horridum* over 700 mm in total length may be considered large; adults approaching 1 m in total length can be regarded as exceptional. Sumichrast (1864) reported total lengths of up to 1.5 m for *H. horridum*, but such an extreme size has never been substantiated. The heaviest Beaded Lizard we have encountered in the field was a robust male *H. horridum horridum* in Jalisco with a mass of 1,600 g and a total length of 783 mm (SVL = 444 mm). The largest individual we have measured was a male *H. h. exasperatum* taken from near Alamos, Sonora (and on display at the Centro de Ecología de Sonora, Hermosillo) with a total length of 858 mm (SVL = 483 mm; plate 29). To our knowledge, the largest *H. horridum* on record is a captive male measuring 991 mm in total length (39 in.) and 521 mm in SVL (R.W.

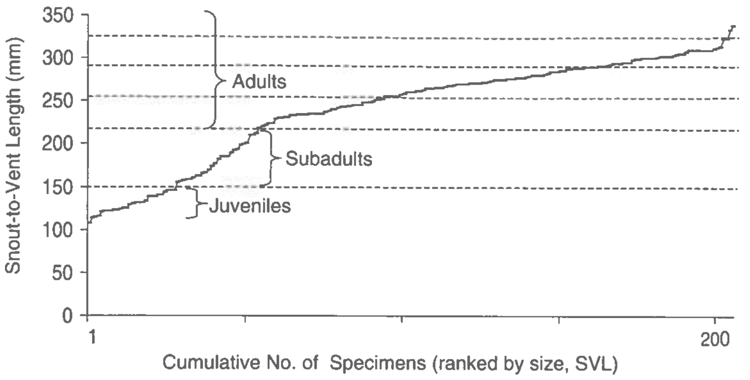


FIGURE 40. Ranked order of body size in 206 specimens of *H. suspectum* captured primarily between 1950 and 1990 in southern Arizona and preserved in the University of Arizona herpetology collection. Dashed horizontal lines depict cutoffs for size classes.

Applegate, pers. comm.). Captive *Heloderma* often weigh much more than similar-sized counterparts in nature, and, because of their low metabolic rates and great storage capacities, it is relatively easy to produce obese individuals through overfeeding. Among the heaviest-ever *H. horridum* was a captive on display at the San Antonio Zoo that, in 1952, measured 780 mm in total length but weighed 4,538 g, or nearly 10 lb!

Bogert and Martín del Campo (1956) noticed a general latitudinal trend of decreasing body size in *H. horridum* from north to south. Mean adult size of the northernmost subspecies, *H. h. exasperatum* (SVL = 353 mm), was slightly larger than *H. h. horridum* (SVL = 345 mm), which was, in turn, slightly larger than *H. h. alvarezi* (mean SVL = 330 mm). Individuals of the fourth and southernmost subspecies, *H. h. charlesbogerti*, from the Motagua Valley of Guatemala, do not seem to reach the large sizes often seen in the *alvarezi*, *horridum*, and *exasperatum* subspecies (J.A. Campbell, pers. comm.). Of the 20 or more specimens examined by Campbell, all have been rather slender and relatively small. However, the specimens within the type series described by Campbell and Vannini (1988) show a mean SVL of 369 mm, which is certainly within the range of the other subspecies. Given the considerable variation in body size (and other characteristics) within populations of Beaded Lizards, great differences in body size among subspecies are unlikely. Whether *H. horridum* actually grow to be increasingly larger from south to north, however, is a hypothesis in need of testing.

SIZE CLASSES AND POPULATION STRUCTURE

The age structure of a population is a very useful characteristic for understanding past and predicting future trends. Because age is difficult to accurately determine in most vertebrates (Castanet 1994), size classes (represented by groups of individuals of similar size that presumably correspond to specific age classes) are often used to portray the structure of a population. We can use what we know of the range in body sizes of helodermatid lizards, and how quickly they grow to a size capable of reproducing (see Growth Rates, below), to assign size classes and present an overview of the structure of *Heloderma* populations.

Two useful patterns emerge when we examine the ranked distribution of sizes (in millimeters of SVL) in a "population" of 206 Gila Monster specimens collected around Tucson primarily between 1950 and 1990 and housed in the zoological collections at the University of Arizona (fig. 40). First, there appears to be a break in SVL between 145- and 155-mm SVL (which we use to split our first two size classes, below), and second, after a SVL of approximately 230 mm, body size increases much slower as additional individuals accumulate in the sample. This leveling-off likely represents the SVL at which Gila Monsters become reproductive and begin shunting energy away from growth in length and into storage and/or reproductive activities. It falls fairly close to 220 mm, a value at which *H. suspectum* was found to become reproductively active based on histological analyses by Goldberg and Lowe (1997).

We can thus consider Gila Monsters having a SVL less than approximately 220 mm to represent juveniles that are not yet capable of reproduction and who shunt all energy not used for maintenance or storage into growth. Based on the evaluation of 56 such juvenile specimens preserved in the collection at the University of Arizona (see above), the group can be split into two size classes; those less than 150 mm (which might be the approximate size that wild juvenile Gila Monsters reach as they enter their first winter) and those between 150- and 220-mm SVL (a group that might be considered subadults). For clarity, we arbitrarily divide the remaining (adult) size range (221-mm SVL and above) into four equally spaced size classes, each spanning 35 mm in SVL (fig. 40).

With size classes established, we can begin to evaluate the structure of Gila Monster populations. The size structure of the "population" represented by the University of Arizona's preserved specimens is shown in figure 41. This sample shows that 27% are nonreproductive subadults and that less than 22% are large adults over 290 mm in SVL.

A different pattern emerges when we examine population size structure from data gathered directly from the field. The best sample of a field population comes from the unpublished studies of Brent Martin and C.H. Lowe from 4 km^2 in southern Arizona between 1979 and 1988 (fig. 42). The size structure generated from their data shows a majority of the sample (70%) as relatively large adults over 290 mm in SVL. Subadult (i.e., nonreproductive) individuals compose less than 10% of the sample. Data gathered from similar-sized sampling areas in Utah (Beck 1985b, 1990) and New Mexico (D.D. Beck and R.D. Jennings, unpublished data) show population size structures that appear even more biased toward the larger-size classes (fig. 42).

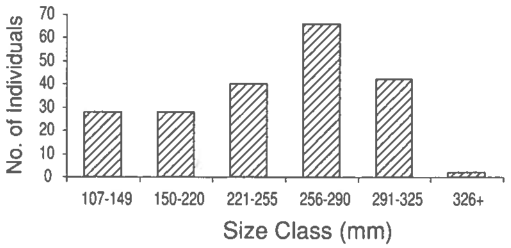


FIGURE 41. Size structure of a *H. suspectum* "population" comprising specimens captured in southern Arizona and preserved in the University of Arizona herpetology collection. The relatively large proportion of individuals in the smaller size classes (107–220 mm) may be an artifact of collecting bias (see text).

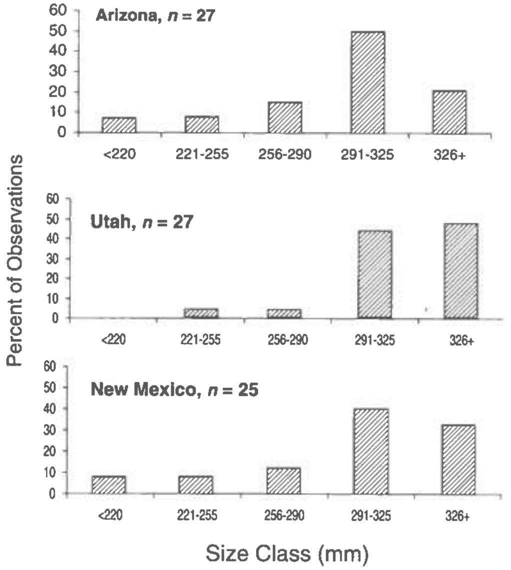


FIGURE 42. Size structures of three *H. suspectum* populations. See text for explanation of size-class categories.

What do these data tell us about past and future population trends? Because smaller size classes are underrepresented in the data from the field, does that suggest that the reproductive potential of such populations is lagging and that they may be in decline? Not necessarily. The population size structures shown in figures 41 and 42 illustrate sampling biases and should be interpreted with caution. The sample from the University of Arizona (fig. 41) is derived largely from animals encountered along roads and suburban developments around Tucson. The juveniles and subadults in that sample were collected primarily by road-cruising at night during summer when this age class is particularly conspicuous, so a good representation of the smallest individuals ended up as specimens in the University of Arizona collection. At our study sites in Utah, Arizona, and New Mexico (fig. 42), juveniles and subadults are not so easily encountered for at least two reasons: (1) they are even more secretive than adults, showing greater nocturnal activity during which they are not as easy to detect on the surface (see chap. 5), and (2) they rapidly grow out of their size class (see Growth Rates, below). The population size structures assume that all size classes show equal probability of being encountered, an assumption that is rarely met and should, therefore, be interpreted with caution.

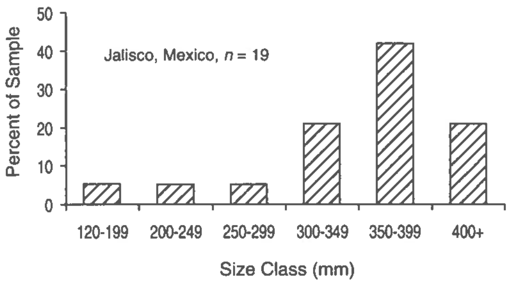


FIGURE 43. Size structures of a *H. horridum* population from Chamela, Jalisco.

Although there is less information available for *H. horridum* populations, size classes can similarly be constructed to represent population structure. Figure 43 shows the structure of a population from Chamela, Jalisco, Mexico. This representation is subject to the same biases outlined above for Gila Monster populations and should, therefore, also be interpreted accordingly.

SEX RATIOS

Of 206 *H. suspectum* specimens that we examined in the collection at the University of Arizona, we observed a sex ratio of 103 males to 93 females, with 10 undetermined, a result suggesting that sex ratios do not deviate significantly from 1 : 1. The North American Regional Beaded Lizard Studbook of all known, captive *H. horridum* specimens gives a sex ratio of 82 males to 71 females for individuals of known sex in zoos and breeding programs in Mexico, the United States, and Canada (Johnson and Ivanyi 2001). Captive data should be interpreted with caution, however, because sex ratios in captive colonies are often intentionally biased.

GROWTH RATES

Helodermatid lizards can grow rapidly. In captivity, hatchling Gila Monsters can show a 2.4-fold increase in total length within their first year, from 160 to 378 mm in total length, and an 11.7-fold increase in body mass, from 34.5 to 403.5 g (E. Wagner, unpublished observations). Captive hatchlings can add up to 130 mm to SVL within this first year and thereby reach reproductive size (although it is unknown whether they actually achieve reproductive *condition* in such a short time). Sexual maturity, however, can be reached within their second year, as noted by Bogert and Martín del Campo (1956). Gila Monsters hatched in captivity successfully reproduce within their third year of life (M. Seward, pers. comm.).

During the 1980s, C.H. Lowe gathered data on growth rates of juvenile Gila Monsters in his laboratory at the University of Arizona. From his data, we found that juveniles (150–220 mm in SVL; 40–200 g) that were fed approximately 300 g/year (mice) showed growth rates approaching 100 mm/year in SVL (up to a 60% increase). One individual increased in mass from 46 to 186 g (>400%) in under 7 months. Growth efficiencies, based on the amount of increase in body mass divided by the amount fed over the same period, were as high as 50%. Growth rates, on average, for this subadult size class were about 50 mm/year in SVL and 80 g/year in body mass.

Heloderma horridum also grow rapidly in captivity. Captive-hatched Beaded Lizards have been observed to show a 3.8-fold increase in mass, from 42 to 159.6 g, in their first year

TABLE 15

Growth Rates of Gila Monsters in Nature Summarized by Size Class

	SIZE CLASS MM SVL	GROWTH RATE (MM SVL/YEAR)	STANDARD ERROR	YEARS TO NEXT CLASS	*n*
1	107–220	38.8	6.86	2.4–3.5	4
2	221–255	34.7	4.78	0.9–1.2	6
3	256–290	14.1	1.46	2.3–2.8	30
4	291–325	7.2	0.64	4.5–5.3	49
5	326–360	2.6	2.22	7.5+	26
6	361+	—	—	—	—

NOTE: As discussed in text. Data are from individuals recaptured at our study sites in Arizona, Utah, and New Mexico.
n = no. of Gila Monsters

(Gonzales-Ruiz et al. 1996). Neonate *H. horridum charlesbogerti* reach adult size (>300 mm in SVL) within 3 years in the laboratory (J.A. Campbell, pers. comm.).

How do growth rates of wild *Heloderma* compare with the rapid rates observed in captivity? There are no records of growth of wild hatchling Gila Monsters, but, in southern Arizona, wild subadults between 150- and 220-mm in SVL show growth rates approaching those of well-fed captives (table 15). Over several decades, we have recorded growth rates of Gila Monsters in nature. These data, summarized in table 15, show that growth rates are variable both among individuals and, especially, among size classes. Some juveniles showed growth rates approaching 50 mm/year, whereas some large adults exhibited no detectable growth over 3 years or more.

From table 15 we can estimate how long it would take Gila Monsters to grow from juvenile to successively larger size classes. A wild juvenile Gila Monster would take, on average, 2.8 years to grow from 110 mm in SVL (the mean size at hatching) to 221 mm in SVL, at which point it would enter the smallest reproductive size class; another year to reach 256 mm (size class 3), 2.5 years more to grow to 291 mm (size class 4), an additional 4.9 years to reach 326 mm SVL (size class 5), and 13 more years to exceed 360 mm in SVL, which is near maximum size. To reach the largest size class (>325 mm in SVL) would, based on our data, take between 10.1 and 12.8 years; Gila Monsters with a SVL over 360 mm would, therefore, be at least 17.6 years old.

Records of growth rates of wild *H. horridum* are rare. Growth rates in SVL of 5 adults recaptured at Chamela ranged from 5.6 to 15.5 mm/year (mean = 10.8 mm/year; Beck and Lowe 1991).

LONGEVITY

There are no published accounts of longevity or survivorship of *H. horridum* in the wild. In captivity, life spans exceeding 38 years have been reported for *H. horridum alvarezi* (Jennings 1984). Of 303 captive individuals noted in the North American Regional Studbook (Johnson and Ivanyi 2001), 23 (7.6%) are over 20 years old and 8 are over 30 years old (all but one of which are males). At the time of this writing, the oldest known living *Heloderma* is a male *H. h. exasperatum* at Zoo Atlanta that entered captivity in 1966 and was at least 37 years old in 2003 (Johnson and Ivanyi 2001; G. Schuett, pers. comm.). These are among the longest life spans recorded for any lizard.

Gila Monsters exceeding 20 years in age are fairly common (Bowler 1977; Jennings 1984). As of May 2002, two captive *H. s. suspectum* exceeding 30 years in age were living in Tucson, Arizona. A Gila Monster at the Prague Zoo lived to be over 29 years old. The oldest *H. s cinctum* of which we are aware was 26 years and 7 months old when it died at the Los Angeles Zoo in 1972; however, there are likely older individuals surviving in captivity.

TABLE 16

Longevity Records of Free-Living Gila Monsters in Southern Arizona

ANIMAL NO.	DATE INITIALLY MARKED	MM SVL	DATE LAST SEEN	MM SVL	DOCUMENTED SURVIVAL (YEARS)	MINIMUM ADJUSTED AGE (YEARS)
62	4/3/82	258	2/24/99	327	17	20.5
39	4/4/80	315	3/31/95	341	15	23.5
58	3/10/82	236	4/1/97	329	15	18
41	4/11/80	194	3/5/93	331	13	15
94	4/30/86	329	3/5/98	339	12	22
103	3/31/87	283	4/13/98	312	11	16.5

NOTE: Based on monitoring of marked and recaptured individuals; B. E. Martin and Lowe 2001.

A perennial question is, how well do longevity records from well-fed captive individuals reflect actual longevity in the field? Table 16 gives records for the oldest known Gila Monsters recaptured in the field. The maximum recorded survivorship to date is No. 62, a male initially captured by Brent Martin in 1982 with a SVL of 258 mm and last recaptured in 1999, 17 years later, with a SVL of 327 mm. At the time of his initial capture, No. 62 was at least 2 years old (based on table 15) and, at 845 g, appeared robust and in good health when, at a minimum age of 19 years, he was recaptured in 1999. Since 1999, the study area has been monitored much less frequently. Given that he was not exceptionally large when he was last seen in 1999 (many Gila Monsters at the site exceed 330 mm in SVL), he may still be alive at this writing (September 2003). Another male, No. 39, captured in 1980 as an adult with a SVL of 315 mm (at least 4 to 5 years old at the time) was last recaptured 15 years later, in 1995, at a SVL of 341 mm, when he was presumably about 20 years old. Based on these observations, we can assume that, in nature, Gila Monsters frequently exceed 20 years of age.

ADULT SURVIVORSHIP AND POPULATION DYNAMICS

Survivorship refers to the proportion of individuals in a population during 1 year that survive to the next. Good estimates of survivorship are difficult to obtain and require consistently monitoring a population for a long time. The unprecedented mark–recapture studies of B. Martin and C.H. Lowe from the 1970s through the 1990s in southern Arizona provide our best estimate of adult survivorship (as well as other population variables) in Gila Monsters (table 17). At one particularly well-monitored site (DBSA) between 1980 and 1999, annual adult survivorship varied from 72.5% (1991–92) to 93.5% (1987–88) (mean = 85%), or, expressed another way, annual mortality/emigration (as evidenced by disappearance of adults from the overwintering site) ranged from 6.5% to 27.5% (mean = 15%). Based on a mortality/emigration rate of 15% per year, an adult Gila Monster would be expected to remain in the population for an average of 6.7 years. If we ignore individuals that were seen only once and never recaptured (perhaps transients), adult Gila Monsters in this population have a mean life expectancy of 7.4 years (fig. 44).

The dynamics of this population are summarized in figure 45, which also illustrates the survivorship of 15 adults (initially marked in 1980–82) through 18 years of monitoring. During this period, the population grew from 15 to 31 individuals, and then fell back to its original number (fig. 45). Recruitment (as evidenced by the number of new animals showing up in the sample each year) varied from 21.7% (1985–86) to 7.7% (1989–90) per year (mean = 14.5%) so

TABLE 17

Population Variables for Adult Gila Monsters

	NO. KNOWN ALIVE	NO. ALIVE FROM 1980–82 GROUP	NO. NEW (RECRUITED)	TOTAL LOSSES	ANNUAL ADULT MORTALITY (%)	ANNUAL ADULT SURVIVAL (%)
1980–82	15	15	15	—	—	—
1983–84	15	11	4	4	13.3	86.6
1985–86	23	10	10	2	6.6	93.3
1987–88	31	9	11	3	6.5	93.5
1989–90	26	8	4	9	14.5	85.5
1991–92	20	4	5	11	27.5	72.5
1993–94	19	4	5	6	15.0	85.0
1995–96	16	3	5	8	21.1	78.9
1997–98	15	3	4	5	15.6	84.4
1999	4[a]	1				
				Mean	15.0	85.0

NOTE: Monitored at an overwintering site (DBSA) in southern Arizona semidesert grassland habitat by B. E. Martin and Lowe 2001.

[a] undersampled during period

that losses were roughly balanced by gains. Even though individuals may be long lived, our limited evidence suggests that populations fluctuate over time.

PREDATION

Helodermatid lizards have many potential predators, but observations of predation on either species are rare. A search for Gila Monster remains in the fecal matter of potential avian (Harris's Hawks, Red-tailed Hawks) and mammalian predators (Coyotes, Kit Foxes, Mountain Lions) turned up only one validated record, in Mountain Lion scats (D. E. Brown and Carmony 1999).

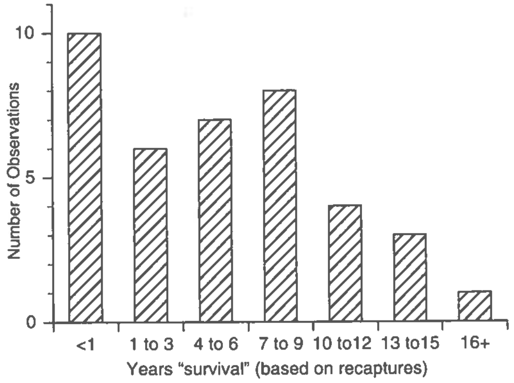


FIGURE 44. Frequency distribution of minimum adult survivorship in DBSA population. Mean survival = 7.4 years (excluding individuals observed only once, i.e., < 1 year).

A rare glimpse into predation on helodermatid lizards is shown in the photograph in plate 30 of a juvenile Gila Monster being swallowed by a California King Snake *(Lampropeltis getula)* near Saguaro National Park east of Tucson, Arizona. As that image confirms, snakes are important predators on *Heloderma,* and juveniles are undoubtedly more vulnerable than adults. Other species of snakes are also known to prey upon Gila Monsters and Beaded Lizards. Funk (1964) observed predation on *H. suspectum* by a Blacktail Rattlesnake, *Crotalus molossus.* Researchers at the field station in Chamela, Jalisco, observed a *Boa constrictor* feeding on a small *H. horridum,* as well as predation by an Indigo Snake, *Drymarchon,* on *H. horridum* (A. Ramírez, pers. comm.).

Prime candidates for important avian predators on juvenile Gila Monsters include roadrunners, hawks, owls, and ravens. Roadrunners and ravens are potentially significant predators on juvenile Gila Monsters. I once observed the severed head of a young Gila Monster tossed off a cliff where ravens were foraging.

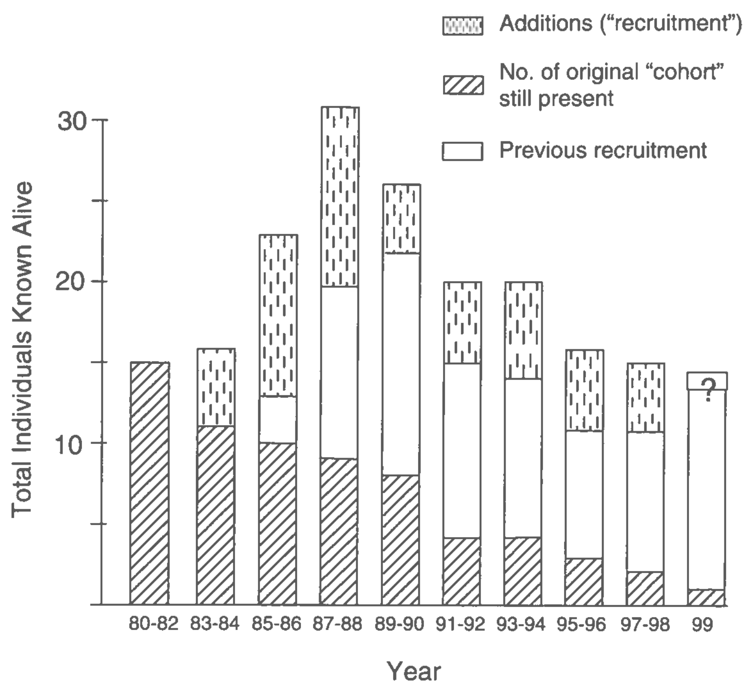


FIGURE 45. Dynamics of a Gila Monster population in southern Arizona. The site was undersampled in 1999 so the population size estimate is left with a "?." See also table 17.

Mammalian predators are also potentially significant, especially coyotes, mountain lions, badgers, bobcats, and foxes. Fecal material of mountain lions in Arizona was found to contain remains of *H. suspectum* (Cashman et al. 1992; D. E. Brown and Carmony 1999). In 2002, keepers at the Arizona–Sonora Desert Museum (located among desert habitat west of Tucson, Arizona) observed a small adult Gila Monster enter an outdoor exhibit housing several coyotes. The coyotes immediately attacked the lizard, tossing it in the air "like Raggedy Andy" and apparently mortally wounding it before keepers interrupted the interaction. It did not appear that the Gila Monster was able to bite any of the coyotes in defense (C. Ivanyi, pers. comm.). The head and neck of a Gila Monster, severed from a healthy adult that was being monitored by researchers using radiotelemetry near Phoenix, Arizona, was thought to be the result of predation by coyotes (Sullivan et al. 2002). A badger was implicated in the death of a radio-implanted Gila Monster north of Tucson (R. Repp, pers. comm.). And, of course, *Homo sapiens* are a most important mammalian source of mortality on *Heloderma* (plate 33; see chap. 9).

POPULATION DENSITY

Although few population estimates have been reported, it has been generally assumed that *Heloderma* seldom reach high population densities (Bogert and Martín del Campo 1956). Near St. George, in southwestern Utah, population estimates of 20 to 25 Gila Monsters per square mile have been determined from intensive mark–recapture studies conducted during the late 1970s and early 1980s (Coombs 1977; Beck 1985b). Such a high population density may be exceptional, and it is doubtful that Gila Monster population densities around St. George remain that high today, given the rapid development in the area over the past 20 years and the resultant displacement of Gila Monsters and loss of habitat (chap. 9).

The Redrock, New Mexico, population, studied intensively during 1992–94, yielded 20 Gila Monsters captured within 4 square kilometers, or approximately 15 lizards per square mile (5 lizards/km²; Beck 1994). That density estimate is similar to the number observed by Martin and Lowe (unpublished data) at their best-documented site in southern Arizona (table 17; fig. 42). Their density estimates (based on minimum known alive) from the DBSA population give us the best idea of how density may change through time. Between 1980 and 1998, population densities ranged from 15 to 31 Gila Monsters per 4 square kilometers (fig. 45).

These estimates of population density may be exceptional; the populations from which they were derived were chosen for study because they were known to be places where Gila Monsters could reliably be encountered and monitored for study. Consequently, the above density estimates should be interpreted with caution. They serve as reference points but should not be indiscriminately applied to other areas containing less favorable Gila Monster habitat.

Because its tropical dry forest environment is more predictable, *H. horridum* likely reaches population densities higher than those of *H. suspectum*. During a field study between 1986 and 1988, I captured 15 Beaded Lizards within an area of approximately 2 square kilometers, which translates to a population density of approximately 23 lizards per square mile. However, based on mark–recapture frequencies, it is doubtful that I had captured many more than half of the individuals inhabiting that same 2 square kilometer area. Population densities of 30 *H. horridum* per square mile are probably not uncommon in undisturbed habitat.

ARE HELODERMATID LIZARDS RARE?

Helodermatid lizards seldom reach the high population densities shown by other reptilian predators, but are they rare? The short answer is that it depends on locality. In some parts of their range (e.g., California and Guatemala), they are very rare. In other parts (e.g., some Arizona upland and tropical dry forest sites) they can be relatively common. One researcher in Arizona encountered 13 Gila Monsters in a single day (J.K. O'Leile, pers. comm.). In other areas where *Heloderma* were once common, they are becoming rare, primarily because of human-caused habitat loss (chap. 9). Throughout much of their range, they are spottily distributed and seldom seen, which certainly gives an impression of rarity.

But rarity is not a simple concept. A species can be rare in several ways, based on its geographic range, population size, and habitat specificity (Rabinowitz et al. 1986; Myers 1997). Each species of *Heloderma* shows a fairly broad geographic distribution (although this could change if *H. horridum* is split into more subspecies; chap. 2). Within that range, however, helodermatid lizards tend to select specific habitats (chap. 5) and show relatively low population densities. These traits certainly tip them toward the rare end of the continuum, an attribute recognized by wildlife regulators in designating legal protection for helodermatid lizards (chap. 9).

SUMMARY OF LIFE HISTORY TRAITS

The size and age at reproductive maturity as well as an organism's number of offspring produced (fecundity) and survivorship are adaptations often referred to as life history traits (Stearns 1992). Life history traits play an important role in population ecology because they can help tell us how rapidly populations may grow (or shrink) and, in some cases, how vulnerable they may be to alterations in habitat, predation pressure, or changes in resource availability. Life history theory suggests that where adult survival is lower, organisms begin reproducing at an earlier age, or, conversely, if adults have a relatively high probability of survival, they may delay reproduction until they are larger and, therefore, capable of greater fecundity (Tinkle et al. 1970; Stearns 1992). This prediction seems to hold for several species of lizards and snakes (Shine and Charnov 1992). How well does life history theory apply to *Heloderma*? Life history traits for *Heloderma* are summarized in table 18. Helodermatid lizards generally fit a long-lived, late-maturing life history pattern, although they seem to have higher rates of survivorship and longevity than expected based on theoretical considerations.

TABLE 18

Life History Traits of Heloderma

Age at sexual maturity	2–3 years
Adult annual survivorship	85%
Longevity	>20 years
Fecundity	Mean of 6 eggs every 1–2 years

The life history characteristics of helodermatid lizards likely developed in response to the variable environments in which they evolved. Even though we often focus on average measures of rainfall, temperature, and resources, for example, there is seldom an "average" year, especially in desert habitats occupied by *Heloderma*. As annual rainfall decreases from tropical dry forest to desert habitats so does its *predictability* and the availability of energy resources. We explore more of the ways that helodermatid lizards cope with this challenge by considering their food habitats.

CHAPTER 7

Diet, Feeding, and Foraging Ecology

> Red Tongue, Black Tongue, fork and spoon
> Darting by day and light of moon
> Sampling chemicals, lapping up eggs
> Flicking from the snout of a snake with legs
> Black on Monster, red on Acaltetepón
> Finding fickle secret scents; nab the nest before it's gone
> Life is ova before it starts
> Pulsing in the tongue of a dry land shark
>
> . . . D. B., *"Fork and Spoon Tongue"*

BOTH SPECIES OF helodermatid lizards feed almost exclusively on the contents of vertebrate nests, a feeding niche shared with few other lizards or snakes. Feeding at nests presents certain challenges. For one, nests are difficult to find. Prudent parents normally take pains to conceal their eggs or offspring in hidden cavities below ground or in branches in trees that are difficult for lizards and other predators to access. Finding such a patchy resource requires considerable searching, keen chemosensory capabilities, and a good memory. Not only are nests difficult to find, but their temporal availability fluctuates strongly in concert with annual cycles of precipitation and drought and with the seasonal reproductive cycles of potential prey. In seasonal environments, a nest predator must, therefore, have an ability to subsist during periods when food may not be available. In some environments inhabited by *Heloderma*, these periods can occasionally be very long. Gila Monsters and Beaded Lizards are well suited to meeting the challenges of feeding on the contents of vertebrate nests. In this chapter, we'll explore the diet and feeding ecology of helodermatid lizards. I'll summarize what we know about the diet of helodermatid lizards and discuss how prey are encountered and eaten. We'll explore how *Heloderma* are able to make use of a feeding niche that few other squamates exploit, and we'll consider what insight might be gained from an understanding of the foraging ecology of the only venomous lizards.

FOOD HABITS

HELODERMA HORRIDUM

As with much of our knowledge about helodermatid lizards, information on the diet of *H. horridum* has been a mixture of embellishment and accuracy, starting with the earliest published observations of Sumichrast (1864). Sumichrast stated that the diet of *H. horridum* "consists essentially of apterous insects [i.e., flies], earthworms, myriapods, and small species of Batrachia, and sometimes even putrefying animal matters. It is fond of the eggs of Iguanas; it is not unusual to meet with it roaming about near the holes dug in the sand, in which these eggs have been left to the action of the rays of the sun." Sumichrast was likely referring to the Green Iguana *(Iguana iguana)*, but he was partly right: Beaded Lizards do roam around the nests of iguanas—or at least Spiny-tailed Iguanas *(Ctenosaura pectinata)*—who place their eggs in sandy, open tropical dry forest habitats. In Jalisco, I have observed Beaded Lizards excavating these nests and have found Spiny-tailed Iguana eggshells in Beaded Lizard guts and feces (Beck and Lowe 1991). Although largely embellished, even Sumichrast's statement about flies, earthworms, and the like may contain a grain of truth; it turns out that *H. horridum* do occasionally eat large insects (see below).

Later, more accurate, observations of the diet of *H. horridum* (based on analyses of gut contents) indicated that bird eggs and nestlings are also eaten (Bogert and Oliver 1945; Zweifel and Norris 1955), as well as juvenile mammals (Bogert and Martín del Campo 1956). Bogert and Martín del Campo (1956) analyzed the food items encountered in stomachs and intestines of 19 preserved *H. horridum* specimens and concluded that bird eggs and fledglings were most commonly eaten (53%), followed by juvenile mammals (32%) and reptile eggs (11%). These early observations confirmed that *H. horridum* is indeed a predator on the contents of vertebrate nests. Pregill et al. (1986) analyzed contents from another five Beaded Lizards (including samples examined by McDiarmid 1963) and found reptile and bird eggs in Beaded Lizard stomachs but also encountered two sets of large beetle larvae. They also reported observations of adult *H. horridum* raiding the nests of Beechey's Jay *(Cissilopha beecheii)* high in trees in Nayarit, Mexico.

In Guatemala, wild *Heloderma horridum charlesbogerti* have been observed to regurgitate shells of large snake eggs (probably tropical racers of the genera *Drymarchon, Masticophis* or *Drymobius*, Campbell and Vannini 1988) and bird remains (possible the dove species *Zenaida asiatica*, Ariano Sánchez 2003). Recently captured individuals have been observed to defecate *Ctenosaura* lizard eggshell fragments (Ariano Sánchez 2003), remains of a small,unidentified bird (Campbell and Vannini 1988), and fragments of large beetles and cockroaches (Ariano Sánchez 2003, Campbell and Lamar 2004). A large cicada was found in the stomach of a subadult *Heloderma horridum charlesbogerti* specimen (Campbell and Lamar 2004).

Of 14 *H. horridum horridum* fecal samples collected by Beck and Lowe (1991) in Jalisco, 71% contained reptile eggs (including those of Spiny-tailed Iguanas), 57% contained feathers (including those of White-tipped Doves, *Leptotila verreauxi*), 36% contained insect parts (although all insects were not necessarily ingested intentionally), and 43% contained both reptile and bird eggs/nestlings. A more recent analysis that I have done on eight fecal and gut samples of wild Beaded Lizards near Alamos, Sonora, and one preserved Beaded Lizard specimen in the University of Arizona Herpetology collection, revealed that most individuals (seven of nine) had eaten lizard or snake eggs ranging from one to four centimeters in diameter, whereas bird remains (feathers; feet of unidentified nestlings) made up a smaller fraction (three of nine) of the specimens. Records of prey items eaten by wild *H. horridum* are summarized in table 19.

The data shown in table 19 confirm that *H. horridum* is predominantly a predator on the contents of vertebrate nests. These lizards are opportunists: nearly any nest that is accessible and manageable may be raided (from aquatic mud turtles to tree-nesting Beechey's Jays) with little regard to size or species. Farmers who live in tropical dry forest near Alamos, Sonora, have told me they have observed Beaded Lizards to occasionally enter chicken coops and eat

TABLE 19

Prey Items of Wild H. horridum

TYPE OF FOOD	SOURCE
JUVENILE MAMMALS	
Cottontail *(Sylvilagus)*	Bogert and Martín del Campo 1956
Cotton rat *(Sigmodon)*	Bogert and Martín del Campo 1956
BIRDS: NESTLINGS AND EGGS	
White-tipped Dove *(Leptotila verreauxi)* feathers	Beck and Lowe 1991
Unidentifiable feathers	Beck and Lowe 1991
Beechey's Jay *(Cissilopha beecheii)* nest	Pregill et al. 1986
Unidentified set of eggs	Pregill et al. 1986
Douglas Quail *(Lophortyx douglasii)*	Bogert and Oliver 1945
Dove egg shells	Bogert and Oliver 1945
13 quail eggs	Zweifel and Norris 1955
Nestling Squirrel Cuckoo	Zweifel and Norris 1955
Feathers; feet of unidentified nestling	D. D. Beck, unpublished data
Foot of dove *(Zenaida asiatica)*	Ariano Sánchez 2003
REPTILES	
Large snake eggs *(Drymarchon, Masticophis, or Drymobius)*	Campbell and Vannini 1988
35 unidentified lizard eggshells	Bogert and Martín del Campo 1956
Foot and part of carapace of *Kinosternon* embryo and eggshell fragments	Bogert and Martín del Campo 1956
Ctenosaura pectinata eggshells	Beck and Lowe 1991, Ariano Sánchez 2003
Unidentifiable leathery lizard/snake eggshells	Beck and Lowe 1991
Two sets of unidentifiable reptile eggs	Pregill et al. 1986
Six sets of lizard/snake eggs (1–4 cm diameter)	D. D. Beck, unpublished data
INVERTEBRATES	
10 beetle larvae between 20 and 30 mm long	Beck and Lowe 1991
Two sets of large beetle larvae	Pregill et al. 1986
Large cicada	Campbell and Lamar 2004
Beetle–cockroach fragments	Ariano Sánchez 2003

NOTE: Identified from analyses of gut contents and fecal material.

chicken eggs. Eggs and nestlings are not eaten exclusively, however, as beetle larvae (and other large insects) are also occasionally represented in the diet of *H. horridum* in nature. Lizard and snake eggs appear to be the most frequently represented prey items, followed by nestling birds and juvenile mammals. The relative importance of these various prey items is yet to be discovered; we might also expect obvious geographic and seasonal differences in the frequency of birds, reptiles, mammals, and insects in the diet of Beaded Lizards.

Interestingly, many gut samples I've examined from wild *H. horridum* contain more than one type of prey item. From Jalisco, 6 of 14 samples contained remains of both nestling birds (feathers) and lizard or snake eggshells (Beck and Lowe 1991). Of eight samples I more recently analyzed from Alamos, at least three contained both squamate eggshells and remains of nestling birds. The presence of different prey items in the same gut sample suggests that individual Beaded Lizards may eat a variety of prey during any particular foraging period.

It is also noteworthy that *H. horridum* occasionally feed on large insects—most commonly, beetle larvae. When offered *Tenebrio* beetle larvae in captivity, one individual *H. h. charlesbogerti* intentionally consumed the insects with "eagerness" (Ariano Sánchez 2003).

I have watched *H. horridum* digging at Spiny-tailed Iguana *(Ctenosaura pectinata)* nests in Jalisco, which are placed in relatively open, sandy areas along the edges of arroyos, and I have identified the leathery remains of *C. pectinata* eggshells in the feces of many Beaded Lizards. A large female *C. pectinata* (SVL = 224 mm; tail = 383 mm) that I found dead on a road on May 11, 1988, contained 20 fully developed eggs weighing a total of 82 g (or approximately 4.1 g/egg). Eggs averaged 27 mm long by 20 mm wide, a size small enough to fit inside the mouth of an adult *H. horridum* without having to be broken beforehand. A nest of 20 *Ctenosaura* eggs would be a significant meal for a Beaded Lizard, comprising approximately 10% of its annual maintenance energy budget (chap. 4). Although Beaded Lizards appear well adapted for eating large meals such as a set of quail eggs or a nest of juvenile mammals (Bogert and Martín del Campo 1956; Herrel et al. 1997), many meals (e.g., small sets of lizard and snake eggs <3 cm long) are relatively small (Beck and Lowe 1991; table 19). The occasional large meal may be more important energetically, but smaller meals may be more commonly eaten. Although meal size appears to vary considerably, we currently have too little information for a complete understanding of the variability in meal size and its consequences for the feeding ecology of *H. horridum*.

HELODERMA SUSPECTUM

The earliest accounts of the diet of *H. suspectum* assumed that Gila Monsters fed upon bird eggs in nature, but these conclusions were based almost entirely on observations of captive individuals consuming chicken eggs (see Bogert and Martín del Campo [1956] for a review). Later, researchers took issue with this assumption as the debate heated up about whether the venom system was used to subdue prey. Tinkham (1971a) went so far as to make the following statement: "There is obviously much wrong with the statement that the Gila Monster feeds largely on eggs in nature. Nature is far wiser than the thoughts of men, and since nature is conservative, the Gila Monster has venomous teeth for a purpose—but not to eat eggs." It turns out that Tinkham was partially correct. Wild Gila Monsters indeed eat more than just eggs, but the purpose of the venomous teeth may have more to do with defense than with subduing prey—whether the prey item is an egg or a relatively large, struggling nestling (chap. 3).

GUT AND FECAL ANALYSES

Analyses of prey items from the gut and feces of wild Gila Monsters, and from items regurgitated from freshly captured lizards, reveal that *H. suspectum* is even more of a strict nest predator than is its sister species, *H. horridum.* Gila Monsters eat a variety of items encountered in

TABLE 20

Prey Items of Wild H. suspectum

TYPE OF FOOD	SOURCE
JUVENILE MAMMALS	
Cottontail Rabbit *(Sylvilagus audubonii)*	Hensley 1949; Beck 1990; Gallardo et al. 2002
Round-tailed Ground Squirrel (*Spermophilus* [prev. *Citellus*] *tereticaudus)*	Shaw 1948b; Stahnke 1952
Rock Squirrel *(Spermophilus variegatus)*	Beck 1990
White-tailed Antelope Squirrel *(Ammospermophilus leucurus)*	Beck 1990
Black-tailed Jackrabbit *(Lepus californicus)*	Vorhies quoted in Tinkham 1971a
Juvenile Pack Rats *(Neotoma albigula)*	D. D. Beck, unpublished data J. Feldner, unpublished observations
BIRDS	
Gambel's Quail *(Lophortyx gambellii)* eggs	Ortenburger and Ortenburger 1926; Arnberger 1948; Jones 1983; B. Sullivan, pers. comm., R. Repp, pers. comm., others
Mourning Dove *(Zenaida macroura)* eggs	Jones 1983; Beck 1990
Curved Billed Thrasher nestings	J. Feldner, pers. comm
REPTILES	
Desert Tortoise *(Gopherus agassizi)* eggs	Hensley 1950; Coombs 1977; Beck 1990;
9 unidentified lizard or snake eggs	Shaw 1948b
Foot and part of leg of Whiptail Lizard *(Cnemidophorus gularis)*	Ortenburger and Ortenburger 1926
Lizard eggs (*Phrynosoma solare* and *Holbrookia maculata)*	B. M. Martin, unpublished observations
Lizard eggs (possibly *Cnemidophorus tigris*)	McGurty 2002
Unidentified lizard eggs	Beck 1986
7 sets of lizard/snake eggs	D. D. Beck, unpublished data

NOTE: Identified from analyses of gut contents, fecal material, and field observations.

vertebrate nests (table 20). These prey include juvenile rabbits and ground squirrels, quail and dove eggs, and eggs of lizards, snakes, and Desert Tortoises. Similar to Beaded Lizards, individual Gila Monsters may plunder more than one nest in any series of foraging bouts. The stomach contents of a Gila Monster examined by Shaw (1948b) contained both a juvenile Round-tailed Ground Squirrel and the leathery shells of nine lizard or snake eggs. Two of 13 fecal samples analyzed from Utah Gila Monsters contained more than one type of prey item (Beck 1986) as did 3 of 18 gut samples from specimens I examined recently at the University of Arizona (table 21).

Of 18 preserved *H. suspectum* specimens (University of Arizona collection) with food in their guts, 39% contained lizard or snake eggs, 22% contained amorphous material (possibly egg contents), 33% contained mammal remains (4 samples of unidentified hair, possibly *Neotoma;* 2 of nestling cottontail rabbits), 5% contained bird eggshells, and 5% contained unidentified remains of nestling birds. Specimens with lizard eggs in their stomachs consumed quantities ranging from 10 to 15 eggs/sample. One dead-on-road (DOR) juvenile specimen with a SVL of 143 mm, collected July 30, had 12 lizard/snake eggs (mean dimensions approximately 8 by 12 mm) in its stomach (table 20).

TABLE 21

Gut Contents of DOR H. suspectum

CATALOG NO.	SEX	SVL	TAIL	TOTAL	DATE OF COLLECTION	GUT CONTENTS
7210	Unk	121	60	181	7/22/58	Unidentified tissue
15542	M	123	58	181	6/11/62	Amorphous material (egg?)
49028	M	143	68	211	7/30/80	12 lizard eggs
46147	M	145	70	215	5/19/79	Amorphous material (egg?)
47033	F	160	74	234	9/24/76	Sand and amorphous material
44321	M	166	81	247	9/28/77	Sand/hair
14143	F	173	85	258	6/18/59	Amorphous material (egg?)
28260	M	185	92	277	3/30/68	Amorphous material; small shell fragment
14489	F	189	71	260	10/7/60	Hair; *(Neotoma?)* skeletal material
28259	F	233	115	348	7/3/68	Amorphous material (egg?)
9500	M	248	129	377	??	6 lizard eggs; *(Neotoma?)* bones
28262	M	269	128	397	9/7/68	Amorphous material (egg?)
24273	F	280	141	421	4/26/68	10 lizard/snake eggs—34 × 18 mm
28263	F	280	139	419	4/9/68	Amorphous material (egg?)
24832	M	291	135	426	5/24/68	15 leathery snakelike eggs
31173	M	294	142	436	8/9/63	6 snakelike eggs, amorphous material
11272	F	300	130	430	5/12/60	Juvenile *Sylvilagus* (cottontail)
44318	F	310	137	447	8/1/81	Hair; lizard egg
37438	M?	—	—	—	4/15/60	*Sylvilagus* hair
46221	Unk	—	—	—	8/22/80	*Sylvilagus* remains

NOTE: Specimens examined from the herpetology collection at the University of Arizona.
DOR, dead on road; Unk, unknown

FIELD OBSERVATIONS

Actual observations of Gila Monsters feeding in nature corroborate the above information obtained from gut and fecal samples. In an extraordinary set of observations, Jones (1983) watched nine Gila Monsters foraging in northwestern Arizona during April through July. These lizards ate eggs from 24 Gambel's quail and 2 mourning dove nests. Interestingly, in only one case were all the eggs eaten from a nest (two mourning dove eggs). In the remaining cases, the lizards ate an average of only 3.3 eggs per nest (nests contained a mean of 7.7 eggs); the largest meal observed to be eaten was 7 quail eggs. B.K. Sullivan (pers. comm.) observed Gila Monsters near Phoenix, Arizona, visiting quail nests on two occasions and attributed the Gila Monsters' not eating all the quail eggs to their being distracted by a human observer. In late April 2003, R. Repp watched one of his radio-equipped adult female *H. suspectum* in southern Arizona swallow eight quail eggs—all the eggs in the nest. Another researcher setting up to photograph a quail nest in Arizona watched a Gila Monster swallow 6 of the 12 eggs within the nest before he removed the lizard. The female quail returned to the nest and successfully hatched the remaining six eggs (J. Hanson, pers. comm.).

Gila Monsters I've observed foraging on mammal and tortoise nests ate the entire contents of nests they encountered. On two occasions, Gila Monsters ate all four juveniles they

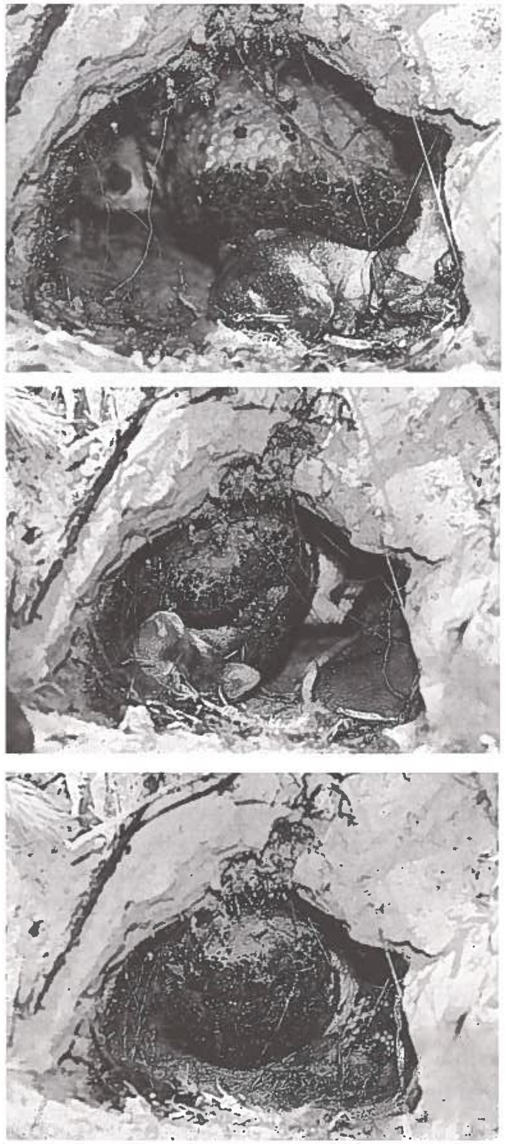


FIGURE 46. Helodermatid lizards occasionally eat large meals. The sequence above shows a wild Gila Monster swallowing one of four cottontail rabbits from a nest it discovered under a creosote bush. The lizard did not appear to use its venomous bite to subdue the helpless rabbits. After swallowing all of the nestlings, which took about 30 minutes, the Gila Monster had consumed a quantity of prey equivalent to nearly one-third of its body mass (photographs by the author).

found in cottontail rabbit nests (fig. 46). I watched a third Gila Monster consume all four eggs encountered in a Desert Tortoise nest in southwestern Utah (Beck 1990). L.I. Gallardo (pers. comm.) witnessed a male Gila Monster eat all the nestlings in a cottontail rabbit nest southeast of Phoenix, Arizona. In southern Arizona, B. Martin (pers. comm.) observed Gila Monsters eating cottontail nestlings as early as January 17. In Nevada, C.M. Gienger witnessed a *H. suspectum* vigorously excavate a kangaroo rat (*Dipodomys* sp.) nest on a sandy mound and consume four nestlings in June 2003.

In April 1990, J. Feldner (pers. comm.) observed a Gila Monster devour the last two nestlings in a Curve-billed Thrasher nest 12 ft up a paloverde tree in southern Arizona. The presumed mother thrasher scolded the Gila Monster, continuing to heckle it as the lizard escaped down the tree.

Field observations of Gila Monsters eating lizard nests are more rare. On two occasions, both in August, B. Martin (pers. comm.) witnessed Gila Monsters excavate and consume lizard eggs. In each instance, Martin removed several eggs from each nest before they could all be consumed, then placed the lizard back at the nest. In one case, the lizard (male) finished eating all the remaining eggs; the other (female) seemed too disturbed to continue feeding. Martin then incubated the eggs; one batch hatched into Regal Horned Lizards *(Phrynosoma solare)* and the other into Lesser Earless Lizards *(Holbrookia maculata)*.

JUVENILE DIET

What little is known about the diet of juvenile *Heloderma* suggests that, as with adults, they also specialize on the nests of vertebrates. One DOR juvenile that I examined in the University of Arizona collection contained 12 small lizard eggs (mean size approximately 12 by 8 mm). Of eight remaining juveniles (SVL >220 mm; chap. 6) in the University of Arizona collection, one contained hair and partially digested skeletal remains of a juvenile mammal (possibly a pack rat, e.g., *Neotoma albigula*), one contained sand and hair, six contained amorphous egglike material, and one contained fragments of bird eggshells (table 21). Stomach contents of two juvenile lizards found dead on roads in Arizona, reported by McGurty (2002), contained complete shells of lizard eggs (possibly *Cnemidophorus*) and a few mammal hairs.

The smaller size of juvenile Gila Monsters and Beaded Lizards obviously constrains the range of prey sizes they can successfully handle, and thereby limits the diet to eggs or nestlings of smaller species of mammals and birds, and smaller snake and lizard eggs. Although such prey are also accessible to adult *Heloderma,* the energetic value of smaller prey items would be proportionately greater for juveniles, so the availability of nests of smaller prey species are particularly important for juvenile *Heloderma*.

BEHAVIORAL INTERACTIONS BETWEEN GILA MONSTERS AND THEIR PREY

Observations of jackrabbits in the diet of Gila Monsters are noteworthy. The only apparently valid record can be traced to an observation by C.T. Vorhies, a noted mammalogist of the early twentieth century, and quoted by Tinkham (1971a). Tinkham stated that Vorhies had collected several Gila Monsters at a site in southern Arizona and, after placing them in a sack, noticed later that several "small jackrabbits" had been disgorged in the sack. Jackrabbit nestlings are precocial; they are born with open eyes, fully furred, and ready to run. In southern Arizona, young jackrabbits weigh around 110 g at birth (Hoffmeister 1986), or about one-fifth the mass of an average adult Gila Monster. (For comparison, newborn cottontail rabbits, which have been documented in the diet of Gila Monsters on several occasions, are altricial and weigh approximately 40 g; fig. 46). Given their size and speed, a nestling jackrabbit would provide not only a significant meal but also quite a challenge for the relatively slow-moving Gila Monster.

Disgorged juvenile jackrabbits, as well as parts of an adult whiptail lizard found in a Gila Monster stomach (Ortenburger and Ortenburger 1926), beg an obvious question: how are rather slow helodermatid lizards able to catch such fast-moving prey? In the confines of captivity, Gila Monsters and Beaded Lizards will readily eat dead adult mice and even rats. but are they fast enough to capture adult rodents alive in the wild? Álvarez del Toro (1982) noted that *H. h. alvarezi* would pursue live rats or young rabbits in captive enclosures, seizing the prey in their jaws and biting "ferociously" until the lizard could swallow it whole. Ariano Sánchez (2003) describes a captive Guatemalan Beaded Lizard pursuing, capturing, and eating small adult rats. Shaw (1948b) reports a captive Gila Monster eating an adult Collared Lizard. Bogert and Martín del Campo (1956) described the feeding response of a Gila Monster after a half-grown mouse was introduced into its cage. In one instance, the Gila Monster promptly seized the rodent and successfully swallowed it; in a second case, a larger rodent escaped and was pursued by the lizard, which, although moving swiftly for a Gila Monster, was no match for the speed of the mouse. In the wild, it is only under exceptional circumstances that fast-moving prey are likely to be eaten, simply because helodermatid lizards are not quick enough to capture most adult prey, and because the majority of foraging activity seems to be focused on stationary prey found in vertebrate nests (see below).

Rare observations of the presence of fast-moving prey in the diet of wild Gila Monsters, coupled with observations of *Heloderma* readily eating adult rodents in captivity, suggest that if fast-moving prey are somehow cornered or otherwise immobilized, wild helodermatid lizards might seize an opportunity to eat them. A juvenile jackrabbit cornered in a nest probably represents the limit of a Gila Monster's ability to catch mobile prey. Regardless of whether they catch mobile nestlings, however, confrontations of a different flavor occasionally arise between helodermatid lizards and the *parents* of their potential prey.

Female Desert Tortoises are known to show outright aggression toward marauding Gila Monsters. Barrett and Humphrey (1986) describe an amazing 100-plus-minute struggle in southern Arizona between a female Desert Tortoise and a Gila Monster attempting to consume the contents of her alleged nest. During the early morning of July 14, 1983, the Gila Monster had excavated a tortoise egg, broken it open, and was lapping up the contents when the tortoise "rushed" at the lizard, ramming and nipping it, and forcing it to retreat to a nearby burrow. Within the next hour and a half, the Gila Monster tried at least seven more times to regain access to the nest, each time being chased away by the tortoise. The tortoise made several attempts to bite the Gila Monster, successfully nipping its tail on one occasion. The Gila Monster also bit the tortoise on the snout, jaws, and a hind leg (the tortoise showed no ill effects from being bitten by the Gila Monster, even six days later). Barrett and Humphrey (1986) observed a second encounter between two different animals a few weeks later in which an adult female tortoise, with neck extended and mouth agape, aggressively evicted a Gila Monster from her den. A similar aggressive encounter between a Desert Tortoise and a Gila Monster was observed in the spring of 2002 by C. M. Gienger (pers. comm.) at a site in the Mohave Desert east of Las Vegas, Nevada.

Ground squirrels (*Spermophilus* spp.) are well known for their energetic antipredator behaviors toward rattlesnakes, which eat their pups (Owings and Coss 1977; Swaisgood et al. 1999). Round-tailed Ground Squirrels have also been observed to mob Gila Monsters and even to bite their tails, drawing blood (R. Repp, pers. comm.). Gila Monsters are potentially significant predators on the pups of ground squirrels. Interactions between adult ground squirrels and Gila Monsters may account for some of the tail scars commonly seen in wild Gila Monsters.

Interestingly, adult pack rats are nearly immune to the effects of Western Diamondback Rattlesnake *(Crotalus atrox)* venom (Perez et al. 1978); however, juvenile pack rats are not immune to being swallowed by Gila Monsters. In March 1992, Jerry Feldner (pers. comm.) followed some Gila Monster tracks down a wash and into a pack rat midden. He watched the Gila Monster excavate a tunnel in the midden and consume several nestling pack rats. Despite Feldner's observations, however, surprisingly few validated records exist of pack rat nestlings being eaten by Gila Monsters even though these two species commonly occur together. Once, when I was examining a pack rat midden in southern Arizona, I observed a female pack rat dash out with several babies hanging from her teats. Perhaps these resourceful rodents use this behavior, or other unknown methods, to avoid Gila Monster predation.

VARIATION IN DIET

The diet of helodermatid lizards likely varies among populations. For example, at both Redrock, New Mexico, and Paradise Canyon, Utah, a significant proportion of the diet consists of juvenile cottontails (Beck 1990, 1994), whereas in some Arizona habitats quail eggs seem to be more frequently eaten (Jones 1983; Repp 2003; B. K. Sullivan, pers. comm.). These apparent differences in diet probably reflect variation in prey availability among the different study sites. Moreover, what constitutes the most frequently eaten prey items will obviously vary seasonally as different prey species reproduce at different times of year. In addition, *Heloderma* habitats show great year–to-year variability in precipitation and consequent primary productivity (chap. 5). This annual variability translates to large year-to-year fluctuations in the amount of energy available for prey species to convert into eggs or nestlings. Good years provide bountiful food; drought years may provide little. We might predict, therefore, that diet will indeed vary from year to year and that a wide range of prey items may be eaten, depending on what is available.

Although helodermatid lizards are specialists on vertebrate nests, they appear to be generalists regarding the kinds of nests they exploit. A diversity of prey species and sizes has been documented in the diets of Beaded Lizards and Gila Monsters (tables 19–21). Although some of these prey items are relatively small lizard and snake eggs, others, such as quail nests and nestling rabbits, are large and provide substantial energy gains per food item. A meal of cottontail nestlings can weigh over one-third the mass of an adult Gila Monster and provide nearly one-third of a Gila Monster's annual energy budget (Beck 1990; chap. 4). Along with

these energy benefits come the basic mechanical challenges of swallowing a large meal or a hard-shelled egg. Egg-eating snakes of the genera *Dasypeltis* and *Elachistodon* have modifications of the jaws, teeth, skull, and even the vertebrae that allow them to efficiently swallow eggs (Gans 1974). Although helodermatid lizards are not so specialized, they do appear to use a few "tricks" to make eggs go down easier.

FEEDING BEHAVIOR

HOW PREY ARE EATEN

Herrel et al. (1997) describe five stages of *H. horridum* eating quail eggs: approach, pierce, uptake, crush, and swallow. A Beaded Lizard first locates the egg, both visually and by tongue-flicking, then rises on its front legs and bites the egg with its front teeth, piercing it without breaking it. The piercing bite may be repeated several times, yet the egg remains intact. During the uptake phase, the lizard maneuvers its jaws around the egg by either flicking the egg in the air or pushing it against an object or the ground. The tongue aids in maneuvering the food object into the oral cavity, but the primary force used during the uptake phase is inertia generated by movements of the lizard's head, neck, and jaws. Such a feeding mechanism, called *inertial* feeding, contrasts with *lingual* feeding mechanisms (using the tongue to deliver food objects into the mouth) shown by most other lizards (Gans 1969; see below). Crushing consists of 10 to 20 small bites with the mouth barely agape as the egg is moved to the back of the oral cavity. Swallowing begins as the tongue is placed in front of the egg and then retracted to push the egg down the esophagus. Eggs are not always completely crushed when swallowing starts even though bite force measurements show that Beaded Lizards can easily crush eggs (Herrel et al. 1997). By piercing eggs before ingesting them, and waiting until eggs are enclosed within the oral cavity before gently crushing them, Beaded Lizards are able to swallow eggs without spilling any contents outside their mouths.

Field observations seem to corroborate these laboratory measurements. As Repp (2003) watched a Gila Monster raiding a quail nest in southern Arizona, he noticed that as each egg was being swallowed, he could hear its shell cracking as it was completely engulfed within the mouth of the Gila Monster. No yolk was spilled in the process. Repp's observations, coupled with the careful laboratory measurements of Herrel et al. (1997), suggest that helodermatid lizards indeed have some interesting behavioral adaptations for eating eggs (plate 31).

Are these behavioral adaptations for ovophagy also accompanied by morphological specializations? Helodermatid lizards have an enlarged external adductor muscle (responsible for closing the jaw), a strengthened skull (in comparison with other lizards), and enlarged maxillary and mandibular teeth. The utility of these structural features for feeding, however, may be secondary to their use in defense (see chap. 3), or they could simply be traits that helodermatid lizards inherited from their varanoid stock (Herrel et al. 1997). If *Heloderma* show morphological specializations for ovophagy, such traits are far subtler than the lizards' behavioral adaptations.

Although *Heloderma* may show considerable finesse when eating quail eggs, such gracefulness may not always be realized when conditions in nature conspire to disallow eggs being swallowed whole. Jones (1983) observed that Gila Monsters feeding at quail nests swallowed eggs whole on only 4 of 86 attempts. I once observed a wild Gila Monster excavate a Desert Tortoise nest and consume four eggs (Beck 1990). The tortoise eggs were too large for the Gila Monster to take into its mouth, so it cracked each egg open by biting it, then lapped up the contents with its thick tongue as yolk and albumin spilled onto the desert sand. This method did not appear particularly efficient as much egg was wasted and a lot of sand was ingested. Given the size of the tortoise eggs, however, the Gila Monster had no other choice. As they finish consuming the liquid contents of eggs, Gila Monsters may also point their snouts upward, apparently enlisting gravity to aid in swallowing.

FEEDING WITH A SPOON AND A FORK

The thick, forked tongues of helodermatid lizards (plate 2) are used not only to help push eggs down the esophagus during swallowing (as described above) but also to spoon up the contents of broken eggs. The tongue of *Heloderma* is thicker than those of snakes and other lizards with forked tongues (e.g., Varanidae and Teiidae). The adaptive role of a flatter, wider tongue morphology as an egg "spoon" awaits investigation by future researchers. The chemosensory role of the forked tongue, on the other hand, has received a bit more attention (see below).

Many lizards, such as the familiar iguanids, use the tongue to capture prey and transport it into the mouth, a process known as *lingual-based* feeding. A lingual-based feeding system is believed to be the ancestral condition in lizards. It is thought to have constrained evolution of the tongue as a specialized chemosensory organ (Schwenk 1993). Other lizards and all snakes (the scleroglossans, which include *Heloderma*) use their jaws (rather than the tongue) to capture prey, a method termed *inertial feeding* (plate 31).

The shift from a lingual-based to an inertial-based feeding system within lizards was an important evolutionary step, one that has been addressed by investigating the cervical musculature of helodermatid lizards (Herrel and De-Vree 1999). The evolutionary shift to use of the jaws in capturing and swallowing prey (as shown by *Heloderma*) seems to be related to an increase in the complexity of the deep (i.e., epaxial) components of the head and neck musculature. Perhaps an even more important evolutionary consequence of inertial-based feeding is that it frees the tongue to be used primarily as a chemosensory organ. This evolutionary step is believed to have resulted in the amazing chemosensory specialization of the forked tongue in snakes and some lizards, including *Heloderma* (Schwenk 1994).

FORAGING ECOLOGY

HOW PREY ARE LOCATED

The tongues of lizards and snakes are indispensable chemosensory organs used not only for foraging, but for locating shelters, communicating among conspecifics, and identifying predators (Cooper 1994; Schwenk 1995). As the tongue flicks the air, ground, and other objects of interest, it delivers chemical information through ducts in the roof of the mouth to the vomeronasal system, or Jacobsen's organ. The forked tongue may allow snakes and some lizards to simultaneously sample two points along a chemical gradient and, in conjunction with the vomeronasal system, identify differences in chemical concentrations between these two points. In this way, the forked tongue is thought to act as a "chemosensory edge detector" that enables one to follow chemical trails of prey and conspecifics (Schwenk 1994, 1995). The specialization of the tongue as a chemosensory organ reaches its peak in varanid lizards and snakes (Schwenk 1995, 2000).

As the closest living relative of the Varanidae, *Heloderma*'s chemosensory prowess is likely similar to that of *Varanus* and snakes. In the laboratory, Gila Monsters are able to distinguish prey chemicals from control substances by tongue-flicking (Cooper 1989) and to locate lost or hidden prey (Bogert and Martín del Campo 1956; Garrett et al. 1996). When mice are bitten by and then taken away from Gila Monsters, the lizards will continue elevated rates of tongue-flicking for at least 45 minutes (and in some cases for over an hour). This is the longest "poststrike elevation in tongue-flicking rate" (PETF) recorded in a lizard (Cooper et al. 1994).

Such tongue-flicking is also accompanied by active searching, suggesting that helodermatid lizards (along with their varanid relatives and snakes) have a highly developed "strike-induced chemosensory searching" response (Cooper and Arnett 1995). Such a response is not compromised when the odor of prey is masked by other (albeit unnatural) chemicals (such as the odor of men's cologne; Hartdegen and Chiszar 2001), nor do Gila Monsters respond to plant chemical odors, or at least to those of carrots (Cooper and Arnett 2001). Even though wild Gila Monsters may never have to search for quail eggs embedded in an odor of "Mennen Skin Bracer" or encounter carrots in the desert, the results suggest that *Heloderma* are skilled at focusing on relevant chemical stimuli and ignoring irrelevant ones. In snakes, the forked tongue allows predators to follow prey trails and it doubtless provides the same services for foraging helodermatid lizards.

FIELD OBSERVATIONS OF FORAGING BEHAVIORS

How do laboratory studies of chemoreception relate to foraging behavior in nature? By observing both Gila Monsters and Beaded Lizards foraging in the wild, I have been struck by the frequency and consistency with which the forked tongue is used to investigate the surroundings. Both species exhibit a slow, stop-and-go foraging behavior as they shuffle the body from side to side while continually tonguing the substrate. Directed ambling is punctuated by frequent stops, which allow a lizard to pause and more thoroughly investigate a particular spot for a few seconds before moving on. In Utah, Gila Monsters forage at a rate of approximately 0.25 km/hour (Beck 1990), and, in Jalisco, Beaded Lizards forage at paces ranging from 0.7 to 7 m/minute (mean = 3.5 m/minute, or 0.21 km/hour; Beck and Lowe 1991). Of course, there is considerable variation in the speed, duration, and extent of these forays. Both species appear quite focused as they forage, often ignoring obstacles in their path, such as rocks and roots, while continually flicking the tongue. On one occasion, a Beaded Lizard I was tracking walked up to me, climbed over my foot, and, without pausing, continued in the same general direction as it explored various fragments of the forest floor. Both species are excellent diggers; I have watched in nature both Beaded Lizards and Gila Monsters dig continuously, for hours at a time, at potential foraging sites such as tortoise, rabbit, or Spiny-tailed Iguana nests. During their foraging, I have also watched Beaded Lizards climb up the vertical trunks of trees and onto horizontal branches, carefully tonguing along the way (plates 2, 4, 22, and 28).

Gila Monsters show many similarities to Beaded Lizards during foraging, except they spend less time climbing into trees. Although lizards seldom backtrack during foraging bouts, their paths usually meander a great deal. A useful method for assessing foraging distances in some habitats is to follow trackways left by lizards walking through sandy areas (fig. 3). Such trackways leave a record in the sand of the microenvironments investigated as well as the amount of backtracking and digging by the lizards (Beck 1986). At my study site in Utah, I followed 150 such trails and found the mean foraging distance on sandy sites to be 213 m (± 13 m). Lizards did not follow a straight line as they foraged; the actual distance of a trail was about 1.5 times the straight-line distance, indicating that nearly half of foraging movements consisted of meandering.

Helodermatid lizards also appear to use hearing to detect both danger and potential prey. As I approached a foraging Beaded Lizard walking through dry leaf litter in Jalisco, I stepped on a branch that snapped. The Beaded Lizard responded to the sound by immediately stopping and pressing its body to the forest floor, remaining motionless until I approached to within two meters, at which time it began to flee. I once watched a Gila Monster in Utah intensely tonguing as it approached a cottontail rabbit nest. When the lizard located the nest entrance, it turned its head, almost as if listening, and seemed to respond to muffled squeaks emitted by juvenile rabbits within the nest by vigorously digging into the nest and, in time, consuming the nestlings (Beck 1986; fig. 46).

FORAGING "STRATEGIES"

The forked tongue and associated ability to follow a chemical trail are believed to have evolved in conjunction with diet and foraging behavior (Cooper 1994, 1997; Schwenk 2000). Helodermatid lizards are slow-moving predators that forage far and wide on the contents of vertebrate nests, yet devote relatively little time and energy to activity. This behavior seems to defy an established paradigm in ecology that describes foraging modes. Foraging behaviors of vertebrate tetrapods (especially those of lizards) have frequently been described as fitting one of two basic modes: *sit and wait* and *widely foraging* (Pianka 1966; Schoener 1971; Huey and Pianka 1981; see G. Perry 1999 and Schwenk 2000 for excellent reviews). Sit-and-wait predators are relatively sedentary and forage by waiting motionless for prey to approach within striking distance before initiating pursuit and capture. They tend to feed less frequently on relatively abundant, mobile prey, and they allocate less energy to activity (~25%–35% of maintenance calories) than do widely foraging predators (Anderson and Karasov 1981; Huey and Pianka 1981; Nagy et al. 1984). Widely foraging predators, on the other hand (also called *active foragers*), search through their environment for each prey item and show a more refined ability to follow chemical trails (Cooper 1994; Schwenk 2000). They spend more time moving and tend to eat hidden, motionless prey. Lizards that forage widely have been shown to invest a greater portion of their energy budgets in activity (Anderson and Karasov 1981; Huey and Pianka 1981; Nagy et al. 1984), and they also tend to have higher standard metabolic rates, even within the same family (chap. 4; Andrews and Pough 1985; Thompson and Withers 1997a). Conversely, reclusive or sedentary predators tend to have lower rates of metabolism (Putnam and Murphy 1982; Andrews and Pough 1985; Mautz and Nagy 2000). This paradigm about vertebrate foraging modes has been built largely around studies of lizard foraging behaviors, although many other organisms seem to fit naturally into one of these two categories (Anderson and Karasov 1981; Huey and Pianka 1981; Nagy et al. 1984; G. Perry 1999). Helodermatid lizards spend over 95% of their time resting in shelters and have among the lowest standard metabolic rates of any lizard measured (see chaps. 4 and 5), yet they still exhibit a widely searching foraging mode. How can this paradox be explained?

In some respects, helodermatid lizards are active foragers. They search widely for the contents of vertebrate nests, and, as described above, they employ their forked tongues and refined vomeronasal system to follow chemical trails, a trait shared by all active foragers (Cooper 1994). In terms of time and energy devoted to activity, however, helodermatid lizards are much more similar to sit–and-wait foragers. Both species are relatively sedentary, partitioning less than 20% of annual maintenance energy budgets to activity (chaps. 4 and 5), and generally have low activity costs, traits they share with sit-and-wait-predators. In addition, helodermatid lizards appear to feed less frequently than most widely foraging lizards and have the ability to take large meals (>33% of their body mass; Beck 1990; Beck and Lowe 1991).

As for many generalizations in biology, the dichotomy between widely searching and sit-and-wait foraging modes is oversimplified (G. Perry 1999; Schwenk 2000) and helodermatid lizards provide yet another example. Scincid lizards do not conform to expectations either; their rather slow-moving stop-and-go foraging behavior prompted Regal (1978, 1983) to suggest an intermediate category of *cruising* to better describe the way skinks forage. Other lizard species may even switch foraging mode depending on what they feed upon (Greeff and Whiting 2000). Such observations, coupled with problems of phylogenetically biased sampling (closely related species tended to exhibit similar behaviors), suggest that a straightforward dichotomy does not adequately explain the diversity of foraging behaviors in lizards and snakes (G. Perry 1999; Schwenk 2000).

How is it, then, that *Heloderma* employ a widely searching foraging mode yet allocate so little time and energy to activity? Not only can helodermatid lizards eat large meals, but they also have high-energy storage capacities. Food storage is directly proportional to body mass ($M^{0.10}$; Calder 1984), and in squamate reptiles metabolic rate (MR) is proportional to $M^{0.80}$ (see chap. 4). The amount of time an animal can subsist between meals is proportional to storage/MR, or $M^{0.20}$. Larger animals can, therefore, subsist longer between meals (Beck 1990). Helodermatid lizards are among the largest carnivorous lizard species in the New World and are well known for their ability to store energy as fat in their sausage-shaped tails and in fat bodies within the coelomic cavity. And because helodermatid lizards have such low metabolic rates, once energy is taken in and stored it is used very slowly (chap. 4).

Their great energy storage capacities and their low metabolic rates enable helodermatid lizards to specialize upon a food resource, the contents of vertebrate nests, which few other squamate reptiles exploit. These traits make frequent foraging activity unnecessary for *Heloderma* and result in a foraging mode that includes some behavioral aspects of a widely searching predator with some physiological aspects of a sit-and-wait forager. The conservative energy use of helodermatid lizards suggests the need for some modifications to the way we think of squamate foraging behaviors. Widely searching predators need not necessarily have high activity costs if large meals are eaten, metabolic rates are low, and storage capacities are high. As a group showing evolutionary affinities that are closer to snakes, the foraging behavior of *Heloderma* might enlighten us about evolutionary patterns of foraging behavior in other squamate reptiles as well.

CHAPTER 8

Reproduction, Behavior, and *Heloderma* in Captivity

WHEN BOGERT AND Martín del Campo's classic monograph was published in 1956, virtually no information existed on the reproductive biology of helodermatid lizards. The secrets of their reproductive cycles slowly began to be uncovered in the 1970s as captive animals occasionally reproduced in zoos and private collections, and in the 1980s as biologists intensified efforts to study them in the wild. Analyses of reproductive cycles of wild populations have been difficult because Gila Monsters and Beaded Lizards are such spectacular animals that few scientists conducting permitted research could bring themselves to immediately kill and preserve individuals captured from the wild. As a result, most specimens that ended up in research collections were held in captivity for an indeterminable amount of time before being preserved. This presented a problem for researchers interested in reconstructing the timing of reproductive events because reproductive cycles are usually severely altered by the artificial conditions of captivity. The solution: analyze only road-killed specimens, or individuals otherwise immediately preserved upon capture from the wild. Results of such an analysis were finally published in the late 1990s (Goldberg and Lowe 1997), and a more complete story of the reproductive cycle was revealed. More recently, field biologists have become interested in analyzing the levels of sex hormones of Gila Monsters being monitored with radiotelemetry, and efforts to monitor nesting patterns and incubation periods in nature have picked up.

Associated with reproductive biology is a range of interesting behaviors, such as combat, pairing, courtship and mating, and several important physiological processes, including spermatogenesis, oogenesis, incubation, egg laying, and hatching. In this chapter, I'll explore the reproductive biology of helodermatid lizards by summarizing what is known of these fascinating phenomena. I'll close with a brief discussion of helodermatid lizards in captivity.

SEXING *HELODERMA* AND SEXUAL DIMORPHISM

Adult helodermatid lizards are notoriously difficult to accurately sex; to the uninitiated, it is very hard to tell males from females. Tinkham (1971a) observed differences between males and females in the morphology of their preanal scales and suggested that males have slightly longer tails than do females, but upon closer scrutiny the patterns he observed have not held up (Seward 2000). Interestingly, female Guatemalan Beaded Lizards *(Heloderma horridum charlesbogerti)* appear to have enlarged preanal scales (Campbell and Vannini 1988; Ariano Sánchez 2003). The method of inserting a probe into the tubular hemipenes of males, safe and accurate with most snakes, does not help one to differentiate gender in helodermatid lizards, because both males and females possess a sinus at the base of the tail that allows the probe to enter to a similar depth. Hemipenal bulges are often readily apparent at the base of the tail in males in reproductive condition, especially in the field, and hemipenes can often be extruded with manual palping from wild-caught individuals. However, these differences are only manifested during the breeding season and may not be reliably observed in captive individuals. Radiographic techniques that allow accurate measurement of the ischium in the pelvis have been used with limited success (Card and Mehaffey 1994). Such analyses have suggested that females have a significantly longer and wider ischium than do males (Card and Mehaffey 1994), yet this has not proven reliable in subsequent analyses (Seward 2000).

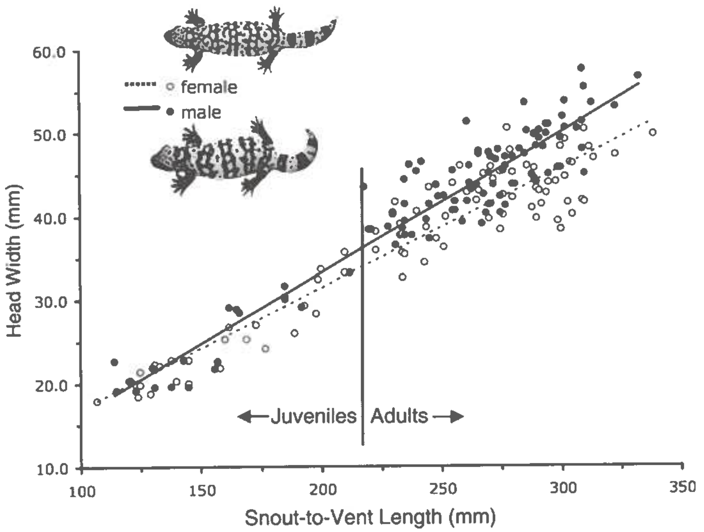


FIGURE 47. As they mature, male Gila Monsters gradually develop significantly wider heads than females (from Gienger and Beck, unpublished ms). General differences in body form are shown at top (photos courtesy of Mark Seward).

Using ultrasound imaging to identify gonads or hemipenes has become a reliable technique for sexing helodermatid lizards; testes in mature males are apparently easy to identify and follicles are visible in ovaries regardless of the time of year at which the examination is made (Morris and Alberts 1996; Seward 2000). Ultrasound imaging of the ventral surface of the tail, just distal to the cloaca, allows one to identify hemipenes, and thereby males (Morris and Henderson 1998). The advent of portable ultrasound units also makes this technique feasible for use in the field.

The question remains, aside from obvious anatomical differences in their reproductive organs, do male and female helodermatid lizards show significant sexual dimorphism? Others have noted subtle differences in body proportions, with female Gila Monsters having slightly longer, rounder ("pear shaped") abdomens than males (Tinkham 1971a; D.E. Brown and Carmony 1999; Seward 2000). This difference, although obvious in some individuals, is highly variable and has yet to be quantified. Some have also noted that males seem to have slightly larger or wider heads than do females (fig. 47).

Over the years, I too had noticed that an apparently larger, wider head in males consistently helped differentiate large males from females in the field. We decided to test this hypothesis by comparing head size in relation to SVL in 194 preserved *H. suspectum* housed in the herpetological collection of the University of

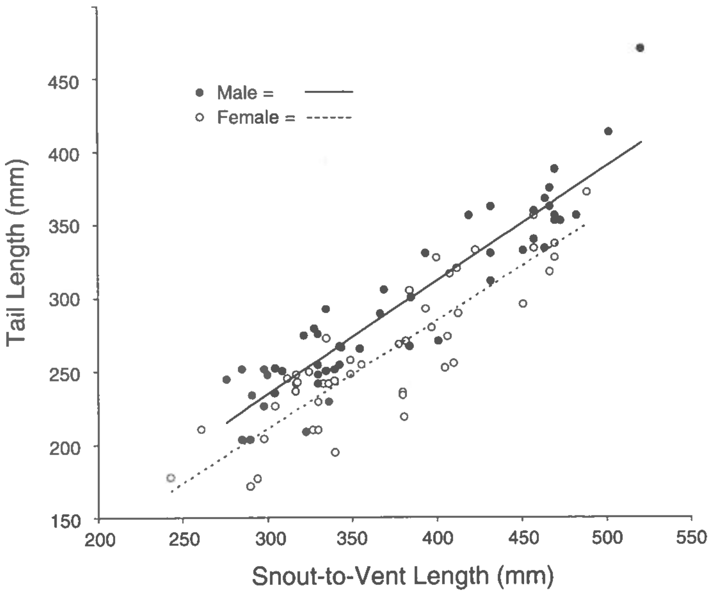


FIGURE 48. Sexual dimorphism in tail length in *H. horridum* (after Gienger and Beck, unpublished ms).

Arizona. We were able to verify the sex of the specimens by dissection and found that males, indeed, have significantly larger heads than females (fig. 47; Gienger and Beck in review). Although this difference is significant statistically, an examination of figure 47 shows that there is considerable variation in head size, even within sexes. Head width also varies with energy status; fatter, well-fed individuals tend to have wider heads. Unfortunately, therefore, head size is not a simple, easy technique for determining gender in Gila Monsters, especially in smaller individuals.

We also found that, based on measurements of 106 *H. horridum* (both alive and preserved), male *H. horridum* have proportionately longer tails than do females (fig. 48; Gienger and Beck in review). Male and female Gila Monsters, on the other hand, do not show significant differences in tail length. In addition to morphological differences, there appear to be metabolic differences between male and female *Heloderma*. By measuring rates of oxygen consumption during activity on treadmills, male *Heloderma* have been shown to have higher aerobic capacities than females (chap. 4).

These examples of sexual dimorphism in helodermatid lizards suggest that sexual selection has played a role in shaping their morphology and physiology. Males with larger heads may be more successful at pressing an opponent to the ground during the intensive agonistic interactions performed by male Gila Monsters. In some other squamates that exhibit male–male combat, males have proportionately larger heads than females (Shine 1978; Vitt 1983; Vitt and Cooper 1985). A longer tail in male Beaded Lizards may allow an individual to form a higher body arch, lean with more force, and increase the chances that it will emerge on top when the arch collapses (Beck and Ramírez-Bautista 1991; see Combat below). Over evolutionary time, lizards with wider heads, longer tails, or superior strength and endurance (associated with a higher aerobic capacity) may emerge more frequently as winners during combat and may thereby enjoy greater reproductive success.

REPRODUCTIVE CYCLES

Life may be ova before it starts, but reproductive cycles begin even before ova (mature female gametes) are formed. Reproductive cycles are sequences of important events that begin with sperm production (spermatogenesis) or egg

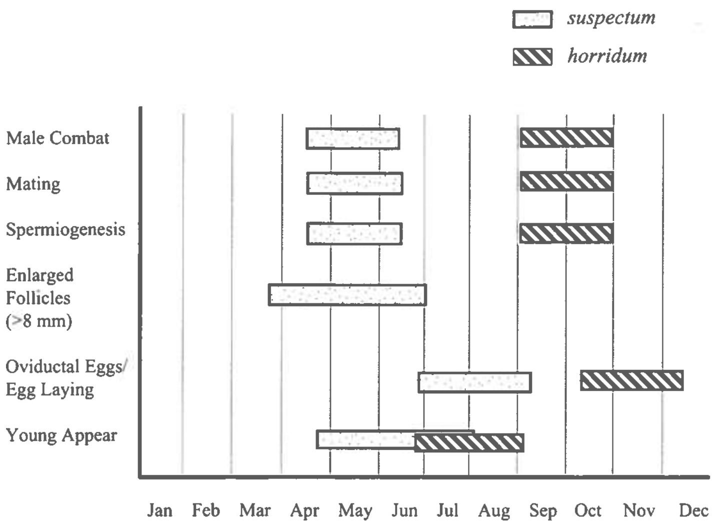


FIGURE 49. Timing of events in the reproductive cycles of helodermatid lizards.

production (oogenesis) and culminate with birth. For most long-lived animals, including *Heloderma*, these cycles are repeated many times during an organism's lifetime. The stages of the reproductive cycle, summarized in figure 49, illustrate the fascinating interdependence of behavior, physiology, and morphology. For example, the physiological process of sperm production is preceded by enlargement of the testes and accompanied by behavioral milestones such as male combat and male–female courtship.

MALE CYCLE

The process of sperm production occurs in the testes, beginning with spermatogonia, which are cells destined to become sperm. Each spermatogonium differentiates into two primary spermatocytes, which, in turn, each give rise to two secondary spermatocytes. Spermatocytes further differentiate to spermatids, and spermatids to mature sperm, or spermatozoa. The final step of maturation from spermatid to mature sperm is termed *spermiogenesis*. As these events are played out, the testes undergo recognizable seasonal changes in size. Four seasonal stages mark events in the testicular cycle of *Heloderma* (after Goldberg and Lowe 1997): (1) Spermiogenesis (testes are at their largest, 4% to 5% of the snout-to-vent length, and spermatids are metamorphosing into mature sperm), (2) regressing (testes are becoming smaller, sperm-producing tissues are depleted, and a few residual sperm still remain), (3) regressed (testes are at their smallest, only about 1% of the snout-to-vent length, and mature sperm are no longer present), (4) recrudesence (testes are increasing in size and primary and secondary spermatocytes are present).

By March, after Gila Monsters have emerged from winter dormancy, their testes are in a state of recrudesence for the upcoming reproductive season (Goldberg and Lowe 1997). Spermiogenesis may begin in April, but it peaks in May when testes are at their largest, lumia of seminiferous tubules are lined with sperm, and the epididymides contains masses of sperm. This period coincides with breeding (see below) and continues through at least part of June. By late June, testes are regressing, and, by July, they have shrunken dramatically and are fully regressed. This condition does not last long, however, as recrudesence begins in September and continues, as long as temperatures permit, through October and November. In most reptiles, spermatogenesis does not occur at body temperatures below 20°C (Saint Girons 1985), so the process is likely suspended in *H. suspectum* during winter months. By the time

Gila Monsters emerge again in late winter, their testes, however, are well on their way to producing sperm for another round of reproduction.

A thorough analysis of the reproductive cycle of *H. horridum* has not been reported. Testicular material examined from road-killed specimens collected in Sonora, Jalisco, and Colima, Mexico (Goldberg and Beck 2001), shows that sperm formation (spermiogenesis) begins in late August and continues through at least early October. This period coincides with the timing of male–male combat in *H. horridum* (see below).

FEMALE CYCLE

The events of the female reproductive cycle include production of egg cells (oogenesis) and addition of lipid-rich yolk that nourishes the developing embryo (vitellogenesis). Eggs originate in the ovary as oogonia, which develop into mature sex cells, or ova. As each ovum develops, it becomes surrounded by a follicle, a structure that mediates reproductive events through endocrine controls. As follicles develop, yolk is also deposited; follicles over about 8 mm in diameter provide telltale evidence that yolk deposition is in progress. Mature ova are shed into the oviduct where fertilization occurs and where eggshell deposition and early embryonic development are played out.

Yolk deposition is in progress in female Gila Monsters by March; follicles become enlarged during late March through May (Goldberg and Lowe 1997). Oviductal eggs appear in May and June through August (Goldberg and Lowe 1997). In Redrock, New Mexico, Gila Monsters contain shelled, oviductal eggs by late June and have been observed to lay eggs in mid-July (D.D. Beck and R.D. Jennings, unpublished data). In Arizona, egg laying has also been documented in July (see discussion of eggs, egg laying, and incubation periods, below). The reproductive cycle of female *H. horridum* has yet to be reported in detail, although it is known that mating occurs in fall and eggs are laid between October and December (Álvarez del Toro 1982; Ramírez-Bautista 1994; see below).

FREQUENCY OF REPRODUCTION

Both species of *Heloderma* can complete their reproductive cycle, from follicle development to egg laying, within one year (Álvarez del Toro 1982; Goldberg and Lowe 1997). Few aspects of the reproductive biology of helodermatid lizards have been observed firsthand in the wild, but analyses of reproductive tissues of specimens preserved immediately after collection (usually road-kills) has yielded some valuable insights (Goldberg and Lowe 1997). Interestingly, Goldberg and Lowe (1997) found that 18 out of 18 female specimens encountered and immediately preserved in March through May either had enlarged follicles, indicating that yolk deposition was in progress, or showed yolk deposition upon closer histological examination. This result suggests that 100% of the Gila Monsters in their sample were preparing to lay eggs during the upcoming summer. This may seem surprising for a long-lived lizard that inhabits a variable environment with low productivity, but it further illustrates the remarkable energetic efficiency of helodermatid lizards.

Does this mean that *Heloderma* in the wild produce a clutch of eggs each year? No, the norm is more likely every other year. Following drought years, or at other times when energy resources are particularly low, females would obviously not be able to acquire sufficient energy reserves to produce a clutch of eggs. Our observations of females tracked with radiotelemetry in New Mexico suggest that they do not lay eggs every year. One female laid eggs in a soil burrow in 1994 and 1995 but not in 1996. Another female carried eggs in 1996 and 1997 but not 1998 (R.D. Jennings and D.D. Beck, unpublished observations). In captivity, Gila Monsters can reproduce every year (Seward 2000), although some breeders find that females reproduce more consistently when bred every other year (Rundquist 1992; Grow and Branham 1996). A large Arizona female legally captured in 1988 was frequently fed while being maintained in a greenhouse in Tucson. She produced clutches of up to seven fertile eggs during each of five consecutive years, 1990–94 (B.E. Martin, unpublished data).

REPRODUCTIVE BEHAVIORS

Little has been published about the social behavior of helodermatid lizards. Gila Monsters and Beaded Lizards show a number of fascinating reproductive behaviors that lend strong support to the notion that they exhibit a structured social system in nature.

FINDING MATES

Gila Monsters may begin searching for mates even before they emerge from winter dormancy. In Arizona, males have been observed entering shelters with females as early as January 21 (R. Repp, pers. comm.). Lizards may forage and feed for a few weeks after late winter or spring emergence, but soon the attention of reproductively active individuals switches largely from acquiring energy to seeking mates. On occasion, finding mates may go hand in hand with male combat. An interesting example of this process in *H. suspectum* is provided by a sequence of behaviors I observed in southwestern Utah.

I began radiotracking a large male (no. 14) along with several other Gila Monsters the previous year and had marked a number of shelters used by these lizards on my study site. As he entered winter dormancy in early November, no. 14 weighed 720 g. He emerged late the following March. Between that time and April 17 (when I watched him exit his shelter, defecate a large stool, and promptly reenter the same shelter) he had obviously foraged successfully. (Coming out to defecate seemed the primary focus of his entire day's activity.) After defecating, he weighed 880 g, having gained 160 g since the previous November! (The stool weighed 40 g and was packed with cottontail, *Sylvilagus auduboni*, hair.) Three days later, I watched no. 14 walk a mile in a single day into a shelter used the previous June by a female I had also been radiotracking.

That journey was different from his typical foraging bouts, which normally involved considerable backtracking and explorations of shrubs and burrows. As he walked that day, no. 14 continually investigated his surroundings with his forked tongue, but his trek was straight and direct. It took him less than four hours to walk a mile (a fairly swift pace for a Gila Monster). I was impressed at the apparent ease and focus with which no. 14 found the distant shelter used previously by female no. 20. I suspected something very interesting was about to happen, so I began monitoring no. 14 even more closely.

Over the next three days, no. 14 visited two other shelters before settling into one I had marked the previous June as being used by no. 18, another large, radio-equipped male (who at the time was not in the vicinity). On April 26, a cool and cloudy day, no. 14 spent the morning and early afternoon moving in and out of his shelter and periodically basking at the entrance, maintaining a body temperature of around 30°C (determined from the temperature-sensing radiotransmitter he was carrying). At 3:00 p.m., another (unmarked) male Gila Monster appeared a few meters downslope of no. 14's shelter. Even though air temperature was only 12°C, no. 14's body temperature was over 30°C (the preferred body temperature; see chap. 4). As the "intruder" approached his shelter, no. 14 boldly made contact and, over the next three hours, the two lizards performed the most spectacular series of behavioral sequences I had ever witnessed in nature (fig. 50).

The morning after he fought with no. 14, the intruder left the area. For the next three days, no. 14 remained in the vicinity of his shelter, emerging occasionally to bask and rub his cloacal area on several lava boulders and grasses near his shelter. On April 29, another (unidentified) Gila Monster crawled into no. 14's shelter and remained with him for a day. No. 14 and the new visitor were visible at times within the shelter, lying side by side with their snouts pointing toward the entrance. No. 14 showed none of the aggressiveness toward this lizard that he displayed earlier toward the intruder. Although I

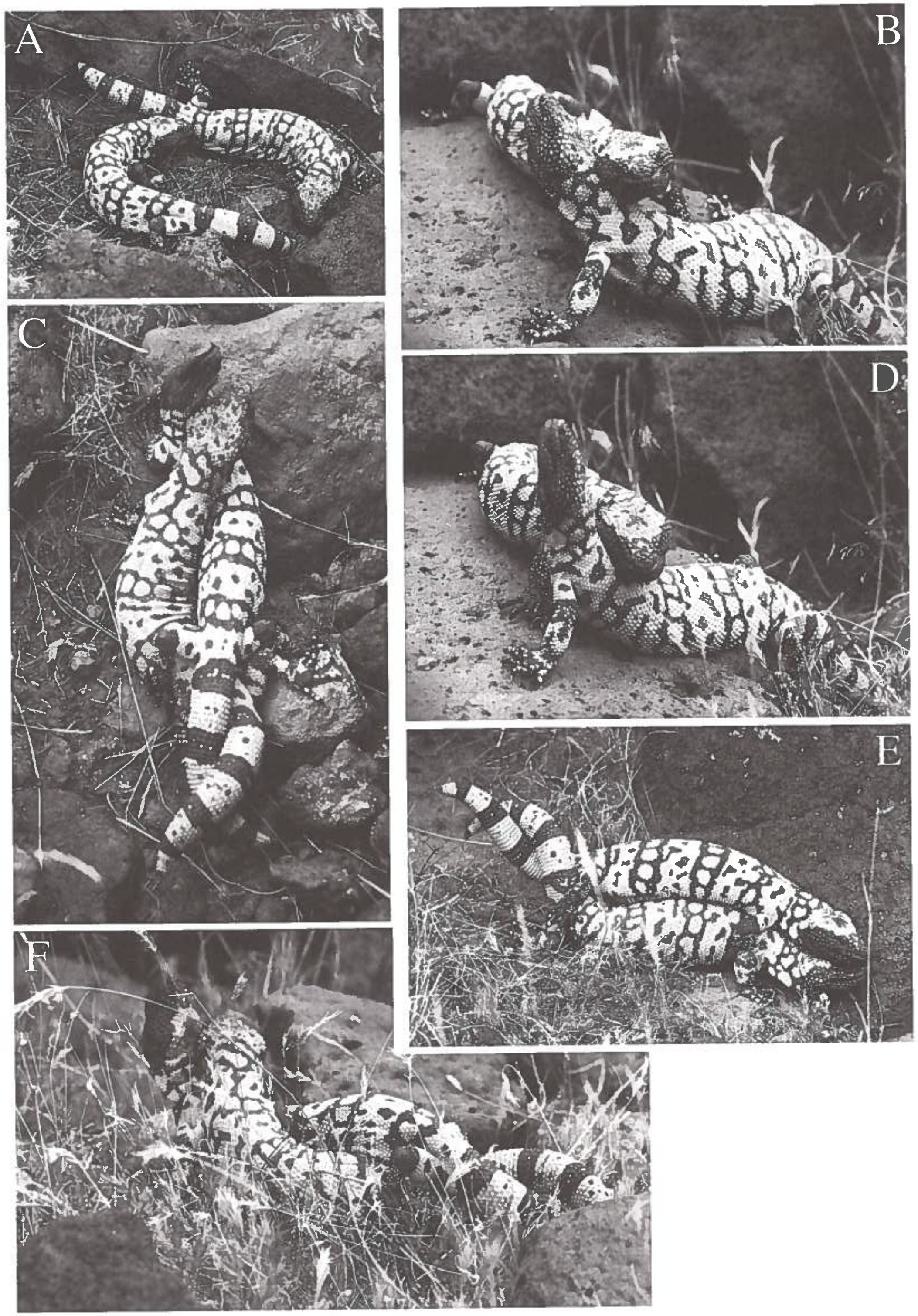


FIGURE 50. Combat sequence of *H. suspectum* taken in the field (photos by D. Beck).

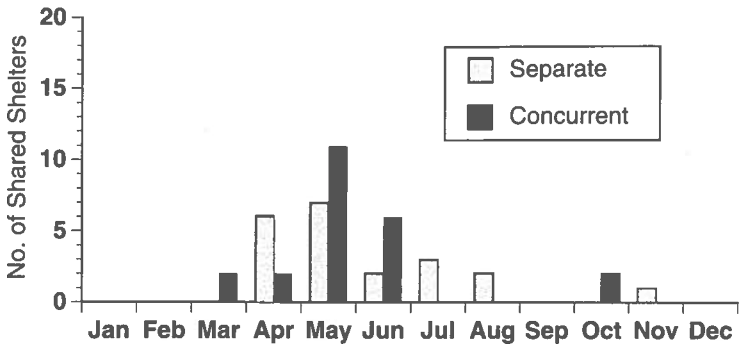


FIGURE 51. Shared use of shelters by five Gila Monsters monitored with radiotelemetry on the Redrock study site during 1992–95. Males and females are most commonly found together in May and June, which coincides with spermiogenesis and ovulation.

was never able to verify the sex of the second visitor, I strongly suspect that the two lizards were mating in the shelter (see Courtship and Mating, below).

This example illustrates how Gila Monsters return each spring to familiar areas used by conspecifics and that shelters are an important, even defendable, resource through which mates are found, and where mating also likely occurs. On our study site in New Mexico, males and females may begin pairing within shelters as early as March; in Arizona this can occur in mid-January. Most pairing, however, occurs in May, which coincides with the time when both sexes are reproductively receptive, sperm production is at its peak, and females are adding yolk to developing follicles in preparation for ovulation (Goldberg and Lowe 1997). A summary of shared shelter use of some Gila Monsters at the New Mexico site is given in figure 51.

Males typically seek out shelters inhabited by females, although females will also enter a shelter with a male. Although males seem to focus on only one female in any given year, they may pair with different females in the same year and pursue different females in different years. Females may also be visited by more than one male in any given year.

The social milieu of spring shelter use can occasionally get complicated and very interesting. Consider a 10-day period in May 1994 at our New Mexico study site. On May 17, male no. 8 entered a shelter occupied by female no. 10, remaining with her until May 24 before moving on to a shelter used two weeks previously by no. 5, another male. At that time, male no. 5 was in a shelter occupied by female no. 2, where he remained for several days. Meanwhile, on May 26, another male (no. 1) moved into the shelter with female no. 10, who remained in the same shelter where she was visited by male no. 8. On May 27, male no. 8 moved into a shelter previously occupied by yet another female (no. 9). Such observations suggest that helodermatid lizards possess an intimate familiarity with their microhabitats and the location of conspecifics (chap. 5). Contrary to what it might seem like to humans, these lizards do not wander aimlessly through their habitats. The following fall, after holding her in captivity for five weeks, we released female no. 2 on the study site. She immediately crawled 150 m into a burrow occupied by male no. 8.

Beaded Lizards look for mates in fall, rather than spring as do Gila Monsters. Little has been reported about how *H. horridum* find mates. At my study site in Chamela, I found them returning to previously visited areas and to reused shelters. Because mate seeking occurs later in the year, some areas visited in fall were in close proximity to overwintering shelters. In one such area at Chamela, we observed combat between two males (see below). As in *H. suspectum*, a keen vomeronasal system and memory likely allow Beaded Lizards to return to familiar territories and locate shelters where potential mates may be found.

How are familiar territories and specific shelters recognized? Associated with their forked tongues and vomeronasal system, helodermatid lizards have a well-developed ability to recognize chemical signals (chap. 7). Scent-marking behavior (such as that shown by no. 14) indicates that chemical cues are used as social signals to identify territories and/or shelters during the mating season. Chemicals deposited within the shelter during occupancy may also be important. Conspecific chemical cues are also used by desert tortoises in selecting burrows during the mating season (Bulova 1997). The fidelity shown to specific shelters suggests that memory is also important. In New Mexico, Gila Monsters show strong fidelity to specific retreats and return to the same shelters year after year (Beck and Jennings 2003). Gila Monsters also use structural cues such as rockiness and depth to identify suitable shelters (see chap. 5). Shelters are, therefore, an important medium in the social and reproductive behavior of *Heloderma.* They constitute a valuable resource that, when a female is in the vicinity and as no. 14's behavior suggested,may at times be defended.

COMBAT

HELODERMA SUSPECTUM

One of the most striking aspects of the behavior of helodermatid lizards is their spectacular ritualized male combat (plate 9; figs. 50, 52, 53; and painting by Carel Brestvankenpen on this book's cover). In both species, the period during which combat occurs coincides with courtship, mating, and spermiogenesis (Ramírez-Velázques and Guichard-Romero 1989; Beck and Ramírez-Bautista 1991; Goldberg and Lowe 1997; Goldberg and Beck 2001)—when both sexes are reproductively receptive.

For an example and some context, let's go back to southwestern Utah where we left Gila Monster no. 14 on April 26. As no. 14 approached the intruder, the two lizards investigated each other with intensive tongue-flicking while moving in a semicircular path around each other (Circling Behavior, fig. 50A). One lizard would shove and nudge the other's head while the other responded by raising or arching its head backwards (fig. 50B and D). No. 14 then climbed on top of the intruder, clasping his forelimbs around the intruder's trunk (Dorsal Straddle, fig. 50E). The intruder responded by raising his head against no. 14's chin, a behavior that no. 14 resisted by pressing his head downward. The tails of both lizards were twisted together and untwisted during this posture. After a few moments of struggling in this position, the intruder turned his head and twisted his body, pressing the side of his head against the chin of no. 14, and no. 14 responded by arching his back and pointing his snout upward (fig. 50C and F). This action resulted in a body twist with each lizard hissing and rocking in an apparent effort to either gain or maintain a superior position. The force generated during the body twist resulted in a sudden separation, like two bent twigs snapping, and the two lizards began circling each other once more. The 2 Gila Monsters performed 13 such bouts over the next 3 hours. Each bout lasted from 4 to 15 minutes and included additional behaviors, including biting, slapping tails, scooping up the opponent with the snout, and arching the back. On occasion, the intruder tried to flee, and no. 14 pursued him and reinitiated additional bouts.

When the fight began, no. 14's body temperature was 33.6°C. As it ended at dusk, hail was falling, air temperature was below 10°C, and no. 14's body temperature had dropped to 17.4°C. Toward the end of the fight, both lizards had trouble righting themselves. Both of their heads were covered with a thin film of blood from biting each other, and both had expended considerable energy in what was obviously a very strenuous activity. The objective during each bout seemed to be to gain a superior position (on top of the opponent) and to press the opponent to the ground. Although both Gila Monsters bit each other during their fight, I was impressed by the ritualized nature of the interaction. It was not a violent "vicious brawl" as combat between Gila Monsters has been depicted in staged (and embellished) encounters shown on television.

Other cases of combat observed in wild Gila Monsters are instructive. At 11:15 a.m. on April 30, 1986, Brent Martin observed two males near Tucson, Arizona, in the midst of combat. As it got hotter, the two adversaries separated and rested in the shade until 4:15 p.m., at which time they resumed their fighting until well after sundown. Presumably, the midday heat curtailed their struggle, which they continued after cooler temperatures prevailed. Martin was fortunate enough to observe a second fight between two different males only 3 weeks later when a brief (25 minute) combat sequence seemed again to be cut short by high temperatures. Within a few meters of the fighting males was a radio-implanted female Gila Monster hidden in her burrow.

In a field study using radiotelemetry in southern Nevada, C.M. Gienger observed two males fighting outside a burrow inhabited by a female on June 3, 2001, at 0753 hours. The "resident" male had spent the previous two days with the female in the burrow. The fight only lasted 18 minutes, after which the "intruder" fled and the resident returned to the burrow with the female where the two remained together for at least one more week. Many of the postures shown by Utah no. 14 and his opponent were witnessed by Gienger, including the Dorsal Straddle, Body Twist, Neck Arch, Head Raise, and Roll. Toward the end of the fight, the intruder bit the resident as the lizards separated from a Body Twist. Similar behaviors were observed in another bout of combat in mid-May, 2003 (C.M. Gienger, pers. comm.). On May 6, 2004, Gienger observed yet another combat session, but this one lasted for 12 hours! (fig. 52). These cases serve to illustrate, once again, an important role of burrows (or shelters) as a medium for reproductive behaviors. They also suggest that male–male combat usually occurs in the presence of a female and that the resident lizard may have an advantage in these tests of dominance.

Male–male combat has also been observed in captive Gila Monsters (Demeter 1986) and is similar to that of free-ranging animals described above. Validation from actual field observations of behaviors exhibited by captive reptiles is rare and illustrates the stereotyped nature of combat in helodermatid lizards. Both in the wild and in captivity, maintaining a superior position and pressing the opponent to the ground appear to be the primary objectives (Demeter 1986; Beck 1990). Combat in captive Gila Monsters has become relatively commonly observed by herpetoculturalists who occasionally allow brief encounters between reproductively active males after they are brought out of overwintering conditions. Some believe they achieve greater reproductive success if they allow male Gila Monsters to fight before mating (Rundquist 1992; Strimple 1995; J. Branham, pers. comm.). Combat in captivity may become vicious, however, with greater biting under conditions where lizards do not have the same options for escape, as do free-ranging animals.

In captivity, female Gila Monsters also exhibit aggressive behaviors toward other Gila Monsters. Especially during the weeks preceding and following oviposition, females become quite defensive and frequently hiss, chase, and bite other lizards (males or females) that approach. These interactions may occasionally result in protracted fights with considerable biting, twisting, and rolling. Some of these fights may even resemble male combat (Neitman 1988); however, females do not normally engage in the extended ritualized postures shown by males (e.g., repeated sequences of the Body Twist, or Body Arch in *H. horridum*, below). When one considers that *Heloderma* feeds on the contents of vertebrate nests, including those of conspecifics, such behavior may not seem too surprising.

HELODERMA HORRIDUM

Combat in *H. horridum* is even more spectacular than in *H. suspectum.* In contrast to the Gila Monster, Beaded Lizard combat occurs during the fall months of September and October (Álvarez del Toro 1982; Ramírez-Velázques and Guichard-Romero 1989; Beck and Ramírez-Bautista 1991). The following description is based on observations of free-ranging *H. horridum horridum* in Chamela, Jalisco (Beck and

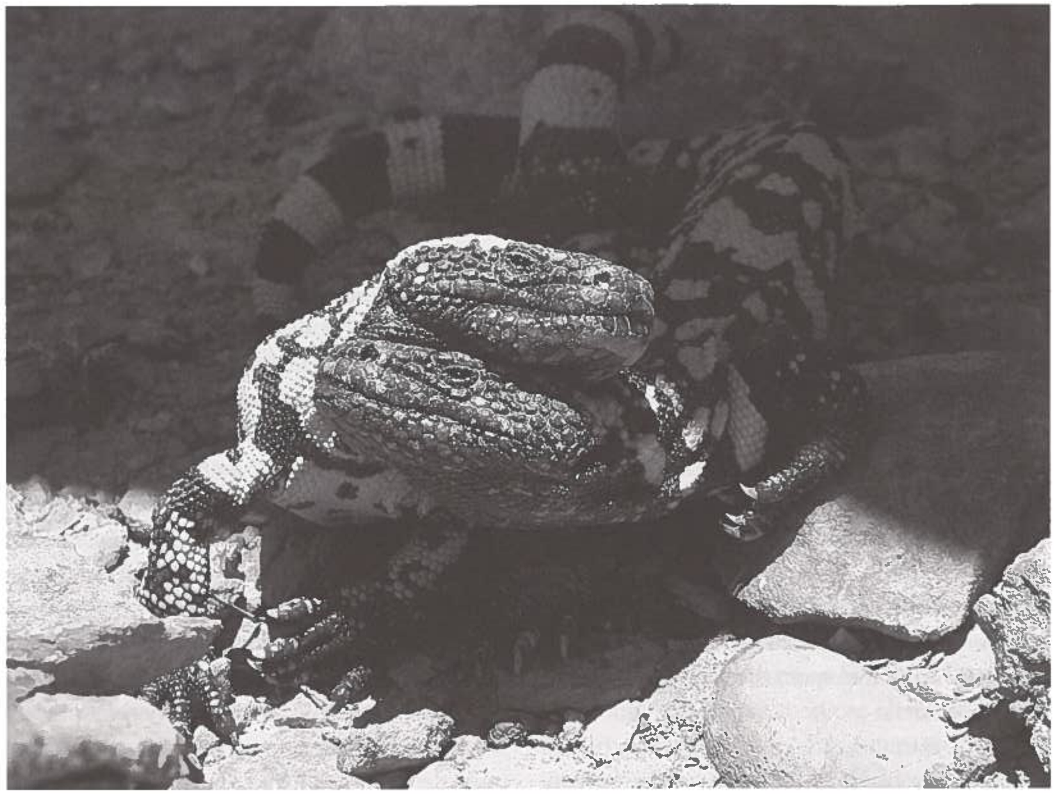


FIGURE 52. In a 12-hour-long contest witnessed by C.M. Gienger in southern Nevada, each of two male Gila Monsters attempts to press his opponent to the ground with repeated bouts of head pressing (above), a behavior countered by the opposing lizard raising his head (below). Photos courtesy of C.M. Gienger.

Ramírez-Bautista 1991), and *H. h. alvarezi* held in outside enclosures at ZooMAT in Tuxtla Gutiérrez, Chiapas (Ramírez-Velázques and Guichard-Romero 1989). Each bout begins as one lizard grasps the other in a Dorsal Straddle, similar to that observed in Gila Monsters (fig. 53a). Lizards may follow each other in a circular pattern (Circling) before initiating the Dorsal Straddle. While in the Dorsal Straddle, the lizard positioned on the bottom (subordinate) flexes its torso laterally, placing a forelimb and hind limb above the pectoral and pelvic areas of the superiorly positioned lizard (fig. 53b). The lizards then press laterally against each other, turning their heads and tails away from each other and pressing their snouts to the ground to begin forming an arch (fig. 53c). Further pressure exerted by the lizards results in a high arch posture (the Body Arch), with venters adpressed and snouts, forelimbs, and tail tips as contact points on the ground (fig. 53d and g). The lizards remain in the Body Arch until pressure eventually collapses the arch, with the dominant lizard ending up on top (fig. 53e and f). Attempts may be made by the dominant lizard to keep the subordinate on his back by biting and pressing his venter against the subordinate (fig. 53f). The arch sequence, as well as termination of combat, appear to be more commonly initiated by the subordinate lizard. After ending up on the bottom after a series of bouts, the subordinate will usually separate and flee.

The objective during each bout is to collapse the arch and force the opponent onto his back. Larger lizards are consistently able to arch higher, shifting their center of mass above the opponent, and lean with greater force. Tail strength and length also appear to be important factors in the ability to form a high arch. Great physical effort is exerted during these combat rituals, and both participants frequently become exhausted. Combat in *H. horridum* may range from one or two bouts lasting only a few minutes to marathons extending over 15 or 16 hours (although such an extreme duration may be a result of confinement). In semicaptive conditions in Chiapas, up to five males have been observed to join in separate contests at the same time, reminiscent of "pitched battles" (Ramírez-Velázques and Guichard-Romero 1989). In Chiapas, male Beaded Lizards frequently carry scars from bites received during combat. Males can often be recognized by their tattered tail tips from repeated participation in the Body Arch (Álvarez del Toro 1982). The apparent advantage of tail length in the ability to form a high arch, and end up on top as the arch collapses, may explain why male Beaded Lizards have longer tails than do females, who do not engage in such ritualized combat behavior.

Gila Monsters and Beaded Lizards show several similarities in their combat rituals, including the Head Nudge, Neck Arch, and Dorsal Straddle, and the primary objective, to press the opponent to the ground, is identical in both species. The most astonishing difference is the formation of the Body Arch by the Beaded Lizard, which is not performed by Gila Monsters. Gila Monsters may have tails (and torsos) that are too short to allow them to effectively form a Body Arch. In *H. suspectum*, it appears the Body Twist serves the same function as the Body Arch of *H. horridum*.

Interestingly, combat in *H. horridum* more closely resembles fighting in monitor lizards, *Varanus*, than in *H. suspectum*. The arching postures of *H. horridum* are strikingly similar to those of *Varanus gilleni* (J.B. Murphy and Mitchell 1974; Carpenter et al. 1976), *V. bengalensis* (Auffenberg 1981a), *V. caudolineatus* (Thompson et al. 1992), and *V. salvator* (Horn 1994; fig. 53). Helodermatid lizards share a more recent common ancestor with the Varanidae than with any other living taxa (chap. 2), and, although they have in common many morphological characteristics, *Varanus* and *Heloderma* differ greatly in several behavioral and ecological traits such as their thermal ecology, levels of activity, and foraging ecology. The strongly similar combat postures of *Varanus* and *H. horridum* suggest that this behavior has been highly conserved in the Varanoidea over its long evolutionary history and likely represent homologous behaviors that occur as a synapomorphy in these

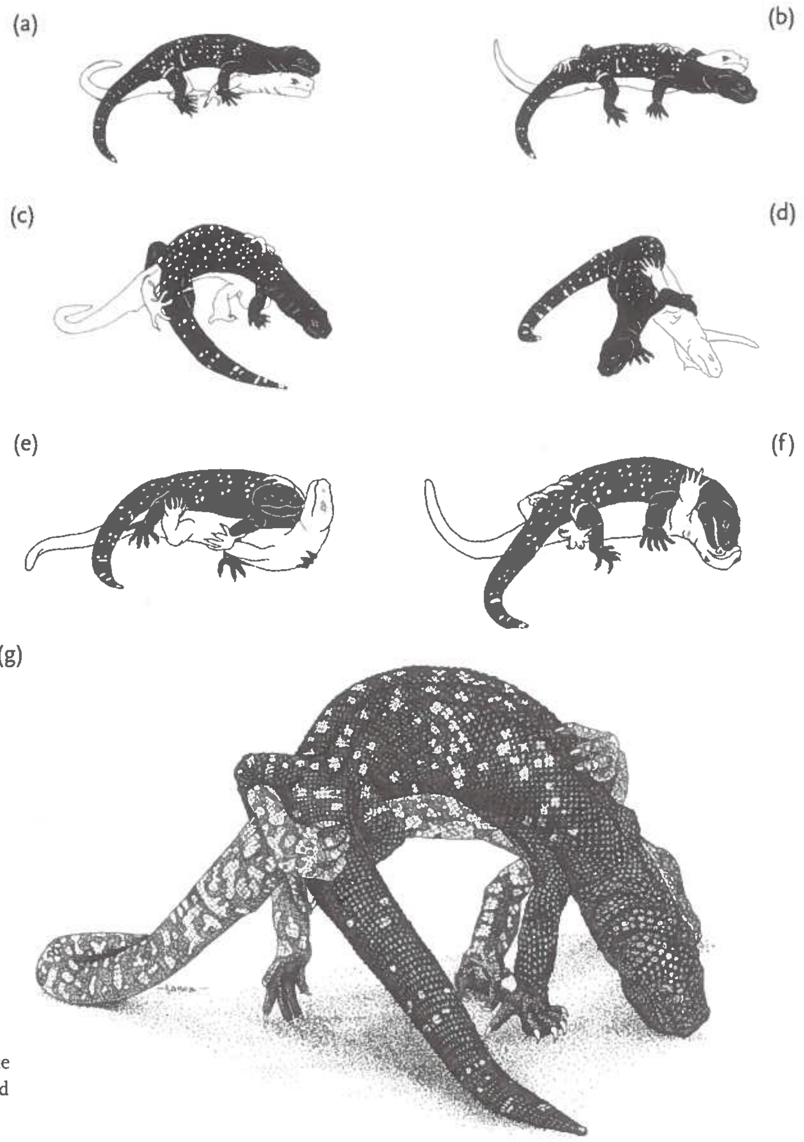


FIGURE 53. Combat sequence in *H. horridum* (after Beck and Ramírez-Bautista 1991).

two taxa. *Heloderma* and *Varanus* are believed to have diverged from a common ancestor at least 80 million years ago (Borsuk-Bialynicka 1984; Gao and Norell 1998, 2000; chap. 2). It is fascinating to contemplate that such a specific and stereotyped behavior as the Body Arch has persisted, independently, in these two genera over this vast period. This serves to illustrate that stereotyped behaviors may survive the eons just as well as certain morphologies and that some behaviors are not as flexible as one might think.

The combat behavior of helodermatid lizards, therefore, holds some interesting evolutionary implications. In the Varanoidea, ritualized grappling postures are more pervasive in agonistic interactions than are the visual displays of posturing, threat, and head bobs exhibited by most other lizard families (Carpenter and Ferguson 1977). The entwining postures performed by *H. suspectum* during the Body Twist (see fig. 50) are reminiscent of those exhibited by crotaline snakes engaged in the well-known "combat dance" (Shaw 1948a; Gillingham 1987). Stereotyped grappling postures are a unique feature of varanoid lizards and snakes and are seldom observed in other squamate reptiles (Carpenter and Ferguson 1977; Beck and Ramírez-Bautista 1991). Combat in varanoid lizards more closely resembles the entwining and grappling behaviors exhibited by snakes and corroborates other evidence suggesting the phylogenetic affinities of these two groups (see Lee 1997).

In summary, male combat in helodermatid lizards is reminiscent of ritualized wrestling matches, whereby participants struggle through various positions to get on top of the opponent and literally press him to the ground. Although the immediate objective during male–male combat is to establish dominance, the ultimate goal is to gain (or retain) access to females and increase one's probability of mating.

COURTSHIP AND MATING

Courtship and mating is a much less showy affair than is male combat (plate 32). In captivity, *H. suspectum* courtship is initiated by the male who, upon approaching a female, will intently explore her body with his tongue. The male may crawl upon the female, rubbing his chin on her head, neck, and back (Wagner et al. 1976; Strimple 1995). Some of these behaviors are reminiscent of head nudging during combat, and combat may occasionally be mistaken for courtship (Applegate 1991). The male may continue his advances for several minutes, continuing to crawl upon the female, tongue-flicking, and rubbing her with his jaw. Occasionally the male will gently bite the female, and, if she is unreceptive, she may bite back or crawl away. If the female is receptive, she will allow the male to hook a hind limb around her pelvis and may twist slightly and raise her tail so that the male may more easily align his cloacal region with hers (Wagner et al. 1976; Strimple 1995; plate 32). Once the male hooks a leg over the female's pelvis, he will align his cloaca and maintain a grip with his hind leg as he inserts a hemipenis (Gates 1956). Slow, convulsive movements, occurring every 3 to 5 seconds, may accompany copulation (Gates 1956). Copulation in captive Gila Monsters may last from 3 minutes (Wagner et al. 1976) to 2.5 hours (Seward 1998).

Details of courtship and mating in free-ranging Gila Monsters have not been reported. Ortenburger and Ortenburger (1926) reported observing a "copulating" pair of Gila Monsters during a hard rain on July 14, just after dark. But, given that testes are regressed and devoid of sperm by July (Goldberg and Lowe 1997), it is questionable that the two Gila Monsters they observed were actually mating.

Mating in wild Gila Monsters more likely takes place out of view within shelters. Male Gila Monsters have been observed engaged in combat near shelters housing females (see above), and male–female pairs are often observed within shelters during April–June (fig. 51), when Gila Monsters are reproductively receptive. At his study site in southern Arizona on May 9, 1986, Brent Martin observed a male Gila Monster encounter a female on the surface, whereupon the male passively followed the female into a nearby burrow. These observations suggest that mating occurs within the privacy of shelters. This may explain why no validated observations exist of wild Gila Monsters mating in the open outside their shelters, and it further underscores the importance of shelters in the reproductive biology of this secretive lizard.

The best accounts of courtship and mating in *H. horridum* come from observations of lizards held in outside enclosures at ZooMAT in Chiapas, Mexico (Álvarez del Toro 1982; A. Ramírez-Velázques, pers. comm.). Before making contact, the male may tenaciously pursue a female for several minutes while she attempts to flee. When the male reaches the female, he climbs on top of her in a dorsal straddle and begins rubbing and stroking the female's head and neck with his chin. The female may actually carry the male some distance before she either escapes or becomes receptive to his advances. The male attempts to shift his tail under the female and align his cloaca with hers. If this fails, he returns to rubbing her head with his chin. Once the female acquiesces, the male raises a hind leg over her coccyx while his other foot rests on the ground (similar to Gila Monster copulatory posture, shown in plate 32). The female may respond by raising her tail. Once the male succeeds in intromission, the two become strongly attached, with the male firmly gripping the female with a hind leg. During mating, the male may gently bite the female on the neck and flick her body with his tongue. Copulation lasts from two to several hours (Arnett 1976; Álvarez del Toro 1982; North 1996).

EGGS AND OVIPOSITION

After copulation, captive Gila Monsters lay eggs in about six to eight weeks (Shaw 1968; Applegate 1991; Strimple 1995; Seward 1998) and Beaded Lizards in approximately eight weeks (Anstandig 1984; Conners 1987; North 1996). Gila Monster eggs measure 24–32 mm wide by 58–64 mm long and weigh 36–40 g (Shaw 1968; Strimple 1995). Clutch size of 17 museum specimens collected near Tucson, Arizona, varied from 2 to 12, with a mean of 5.7 (Goldberg and Lowe 1997). When eggs are first laid, they are opaque and turgid but may become slightly dented and discolored as hatching approaches.

In captivity, Beaded Lizards deposit between 2 and 22 eggs in a clutch, with the reported mean number of eggs ranging from 7 to 9 (Arnett 1976; Anstandig 1984, 1987; Conners 1987, 1993; Gonzales-Ruiz et al. 1996; North 1996; J.J. Perry 1996; Johnson and Ivanyi 2001). Egg size varies from 28 to 37 mm wide by 64 to 72 mm long (Arnett 1976; Anstandig 1987; Conners 1987; J.J. Curtis 1949; J.J. Perry 1996), and viable egg mass varies from 34 to 49 g (J.J. Perry 1996).

Two of the least understood aspects of the reproductive biology of *Heloderma* are its egg-laying habits and its nest environment. Although the opportunity to closely monitor a *Heloderma* nest in nature has so far eluded herpetologists (as of 2004), recent field observations shed some light on the timing of egg laying and the characteristics of the nest. At our Redrock study site, we observed a gravid female emerge from a soil burrow in late July 1994 weighing 240 g lighter than when she entered the shelter (Beck and R.D. Jennings, unpublished observations). The burrow was in a gravelly/sandy area that the female had visited the previous year, and we suspect the female laid her eggs in that burrow. Although we did not monitor the burrow closely enough to witness hatchlings emerge, we did see Gila Monster eggshells, apparently exhumed from the burrow, at its entrance the following June. That same month (in June 1995), the same female returned to a similar burrow 10 m away, where we believe she laid eggs once again. The same burrow system was also used by a second gravid female who emerged in July 1995, having lost weight apparently after laying eggs (R.D. Jennings and Beck, unpublished observations). In 1996, the burrow system appeared to be abandoned by the females. On June 1, 1996, a third female (no. 18) contained ovarian follicles approximately 2 cm in diameter. The following year, on June 27, 1997, female no. 18 contained five shelled eggs in her oviducts. In hopes of discovering where she would lay her eggs, and monitoring temperatures within a nest, we placed a miniature, temperature-sensing radiotransmitter within the most distal egg in one oviduct. Unfortunately, the female aborted the egg on her way back to the study site and we were unable to monitor her nest.

DeNardo, in Arizona, obtained convincing evidence of oviposition in early July (see below). R. Repp and G. Schuett observed a female in southern Arizona emerge from a shelter on July 15, 2002, weighing 202 g less than the previous week, and they strongly suspected the soil burrow was a nest site (pers. comm.). Based on these field observations, and analyses of reproductive tissues by Goldberg and Lowe (1997), free-living *H. suspectum* appear to lay eggs from late June to August, which coincides with the onset of summer rains in the Sonoran and Chihuahuan deserts. Egg laying at this time may increase the probability that sufficient soil moisture is available for the developing embryos. The adaptive significance of the timing of oviposition with summer monsoons, however, has yet to be investigated; it is certainly a question worthy of future study.

THE PUZZLE OF THE INCUBATION SCHEDULE

In nature, *H. suspectum* lay eggs during July or August yet hatchling Gila Monsters do not emerge from the nest until nearly a year later. The earliest dates at which hatchling Gila Monsters have been observed in nature are in late April (Lowe et al. 1986; Goldberg and Lowe 1997; B. Martin, unpublished data). It is far more common, however, to see hatchling-sized Gila Monsters in May, June, or July, which is nearly a year after eggs have been laid. To my knowledge, a wild hatchling Gila Monster has yet to be encountered in fall. If the eggs don't hatch until spring, this pattern suggests an incubation period of 8–10 months, or 240–300 days, for wild *H. suspectum*. In captivity, incubation periods for *H. suspectum* range from 114–152 days at temperatures of 27°C (81°F) to 35°C (95°F) (Shaw 1968; Wagner et al. 1976; K.H. Peterson 1982; Lawler and Wintin 1988; Neitman 1988; Applegate 1991; Rundquist 1992; Strimple 1995; Seward 1998). At a constant 26°C (79°F), the mean incubation time is 140 days (range = 133–147 days, $n = 7$ clutches; M. Seward, pers. comm.). Why is there such a disparity between apparent incubation periods of wild Gila Monsters and those observed in captive lizards?

Some herpetologists believe that eggs of wild Gila Monsters actually hatch in fall after four or five months of incubation, but the hatchlings remain in the nest throughout winter, waiting until spring to emerge on the surface. Others believe the eggs overwinter and do not hatch until soil temperatures in the nest warm during the following spring after at least eight months of incubation (Lowe et al. 1986). Such an incubation schedule is not unprecedented, but it is unusual for a lizard.

At his study site in Arizona upland habitat north of Tucson, Arizona, Dale DeNardo, of Arizona State University, observed a female Gila Monster emerge from a pack rat midden (on July 10, 2001) that she had occupied continuously since mid-June. After emergence, previously palpable eggs were no longer present and she weighed 265 g less than when she entered the midden. Suspecting the site was a nest, DeNardo surrounded it with aluminum flashing and pitfall traps to capture hatchlings as they wandered away from the nest site. On May 4, 2002, nearly 10 months later, the first hatchling dropped into a pitfall bucket. Over the course of summer, four more hatchling Gila Monsters were captured in the pitfall trap, on June 9, June 26, July 1, and August 4. Interestingly, the masses of the neonates at capture decreased, with the last lizards weighing nearly 10 g less than the first neonate caught. This result suggests that Gila Monster eggs all hatch around the same time, but hatchlings remain in or near the nest for weeks, even months, after they hatch. However, we still do not know when the eggs hatch—do they overwinter in the nest or do they hatch in fall?

The answer to the question of the incubation schedule may lie in the temperatures at which eggs are incubated. Temperatures experienced within a *Heloderma* nest in nature will obviously vary from site to site (and year to year), but they are unlikely to remain as warm or as constant throughout the incubation period as those typically used to incubate eggs in captivity. Consider a clutch of eggs laid in a burrow in mid-July when mean shelter temperatures would be 28°C (82°F) to 29°C (84°F) (based on data from our study site in southern New Mexico; see discussion of thermal biology, chap. 4). By early October (10 weeks into incubation), burrow temperatures would have fallen to around 24°C–25°C (75°F–77°F), then to 19°C (66°F) in November, and, by early December (when the eggs would be ready to hatch at a constant incubation temperature of 26°C), burrow temperatures would have dropped to 15°C (59°F) or below. Such a reduction in egg temperature might greatly slow, or arrest, development. Embryos of many reptiles from seasonally cool environments tolerate exposure to low temperatures for extended periods, especially later in development (Packard and Packard 1988). The primary effect on the embryo is to temporarily arrest development and prolong the incubation period

(Packard and Packard 1988). There is evidence that *Varanus komodoensis* eggs take only two months to hatch under certain controlled conditions but eight months under natural conditions (Auffenberg 1988). Eggs of *Varanus salvator* take from 2.5 to 10 months to hatch depending on local conditions (Auffenberg 1988).

To solve this puzzle for *H. suspectum*, M. Seward is investigating the effect of temperature on incubation periods of Gila Monster eggs. Seward has incubated some clutches of eggs laid by captive Gila Monsters at temperatures that closely match Gila Monster burrow temperatures recorded in nature (based on soil temperature data from our study site in Redrock, New Mexico [fig. 20] and DeNardo's site north of Tucson, Arizona). The results of these studies might prove helpful in resolving the mystery of the incubation period. Meanwhile, field biologists continue the quest to monitor a nest in the wild.

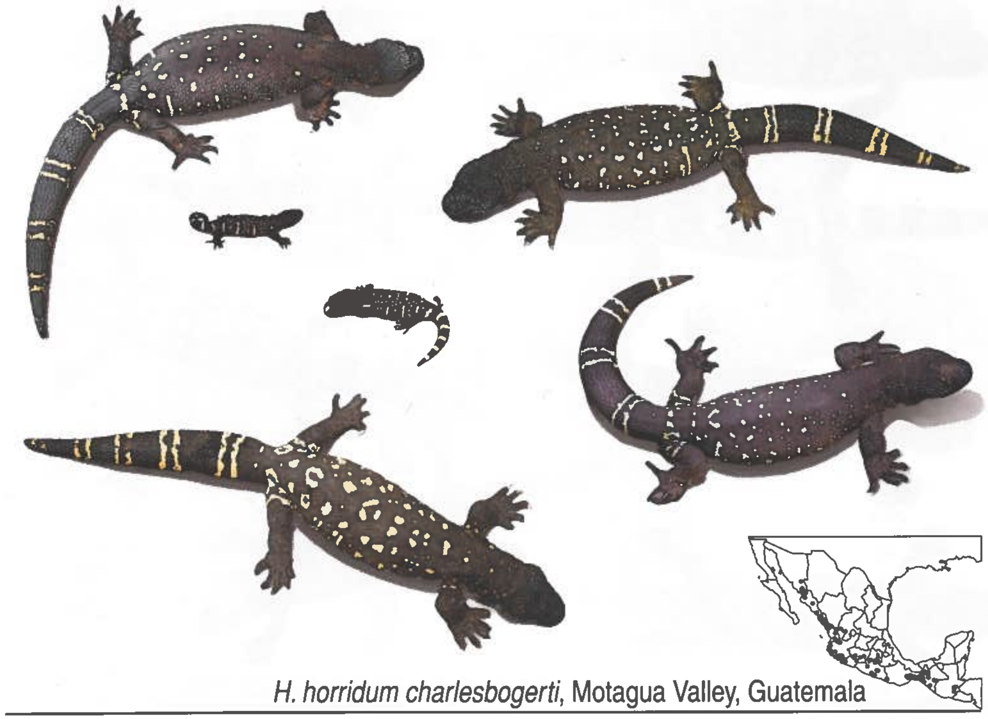
We won't fully solve the puzzle of the incubation schedule until temperatures and hatching are monitored in an actual nest. If eggs stay warm enough in nest burrows throughout fall, it is reasonable to assume that they would hatch in fall. Yet if nest temperatures cool down to the point where development is arrested, especially late during the incubation period, it is possible that incubation would be extended considerably and the eggs would not hatch until soil temperatures warm up in spring. Even after a nest is monitored in nature, however, seasonal and spatial variability in the nest environment may leave the door open to either scenario, depending on the temperature of the nest and the temperature threshold for development of *Heloderma* embryos.

As with Gila Monsters, Beaded Lizards show a similarly long period between egg laying and emergence of juveniles. In nature, *H. horridum* deposit eggs in late fall between November and December. The young emerge with the onset of summer rains in June or July the following year, suggesting an incubation period of 210 to 270 days (Álvarez del Toro 1982; Ramírez-Velázques and Guichard-Romero 1989; Ramírez-Bautista 1994). Incubation periods for *H. horridum* in captivity range from 154 to 226 days at temperatures ranging from 29°C (84°F) to 21°C (70°F) (Arnett 1976; Anstandig 1984, 1987; Conners 1987, 1994; Applegate 1991; Gonzales-Ruiz et al. 1996; North 1996). Incubation times seem to depend on temperature (S. Angeli, pers. comm.). Of ten clutches incubated at 26°C (78°F–79°F), incubation times ranged from 201 to 215 days whereas at temperatures of 27–28°C (80°F–82°F), incubation times ranged from 168 to 192 days (S. Angeli, pers. comm.). Interestingly, the disparity between incubation periods of captive lizards and field observations is much less for *H. horridum* than for *H. suspectum*. Part of this may be because of the lower temperatures at which *H. horridum* eggs have been incubated by some of the more successful captive breeders (e.g., Applegate 1991). However, when incubated at a constant temperature of 26°C (78°F–79°F), *H. suspectum* eggs take, on average, 140 days to hatch while eggs of *H. horridum* take considerably longer (208 days).

HATCHING AND HATCHLINGS

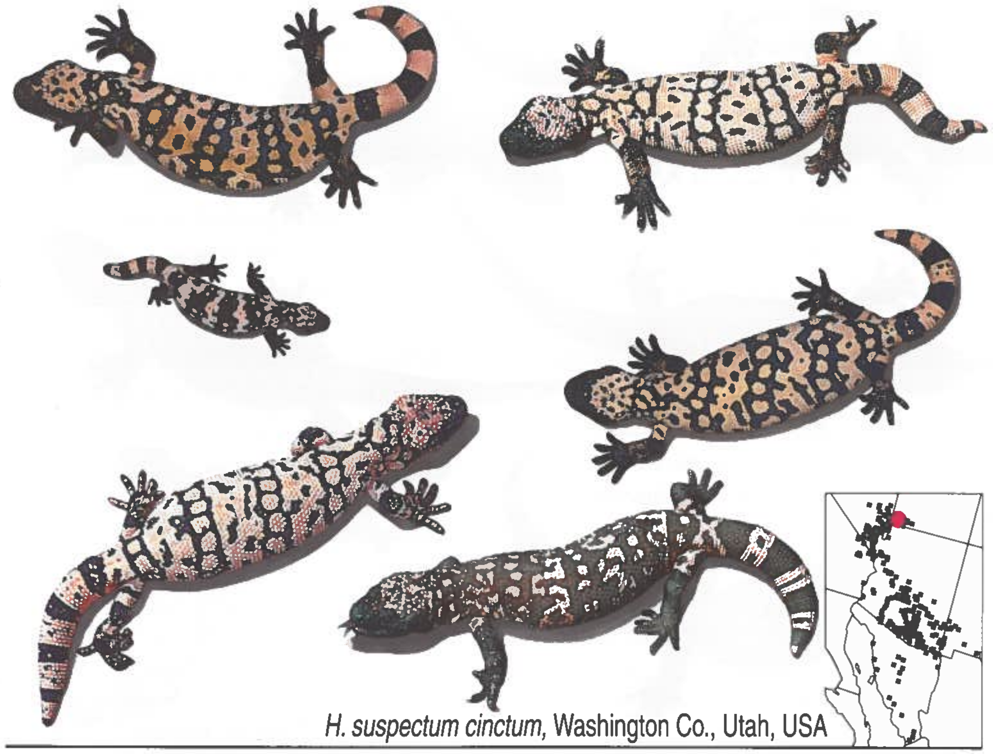
Hatchling-sized Gila Monsters have been observed in nature between late April and August. At his study site north of Tucson, Arizona, Brent Martin observed a hatchling Gila Monster on April 28, 1989, within the burrow of a kangaroo rat mound where a tagged female had possibly placed her nest the previous three years (B. E. Martin, unpublished data). Between May 4 and August 4, 2002, Dale DeNardo and his students at Arizona State University captured five hatchling Gila Monsters that had emerged from a pack rat midden in which a female had laid eggs the previous summer (discussed above). The neonates weighed between 23.1 and 33.4 g and were 135 to 141 mm in SVL. Neonates that emerged later weighed considerably less despite being of similar length, suggesting that neonatal Gila Monsters rely on considerable yolk stores during their first weeks of life. Lowe et al. (1986) found that neonate

H. horridum alvarezi, Tuxtla Gutiérrez, Chiapas, Mexico

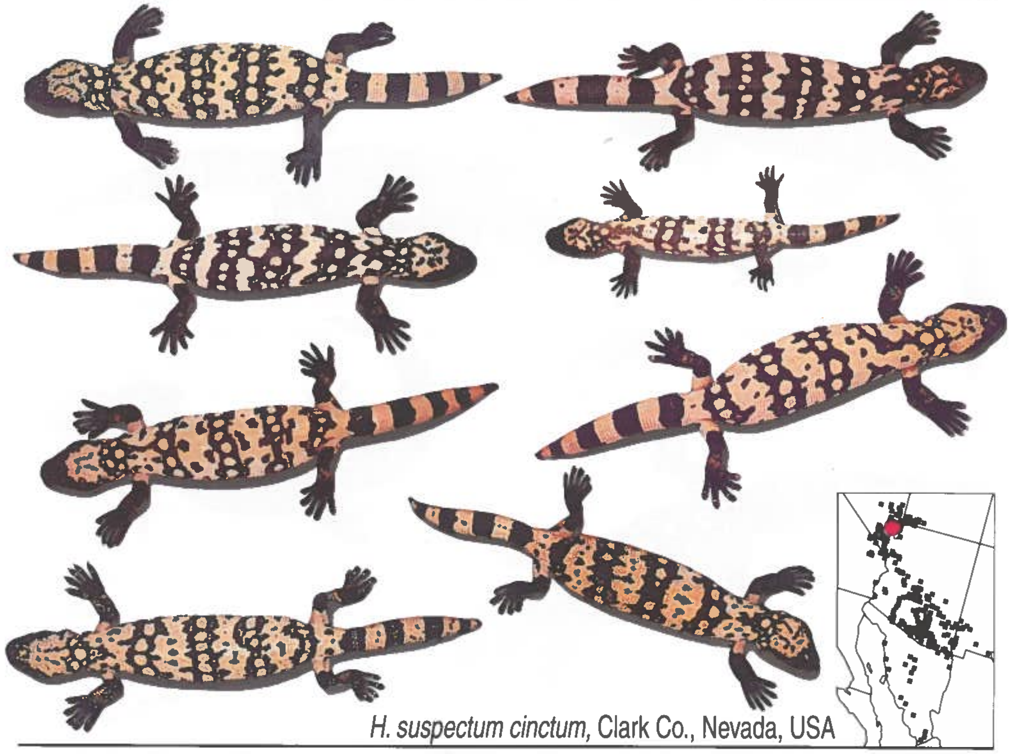


H. horridum charlesbogerti, Motagua Valley, Guatemala

PLATE 14. Portraits of populations: These photographs show a typical range in variation of dorsal patterns within populations of two subspecies of Beaded Lizards. Note the uniformly slate black tails in most adults of *H. h. alvarezi* (top) and the very distinctive tail banding of *H. h. charlesbogerti* (bottom).



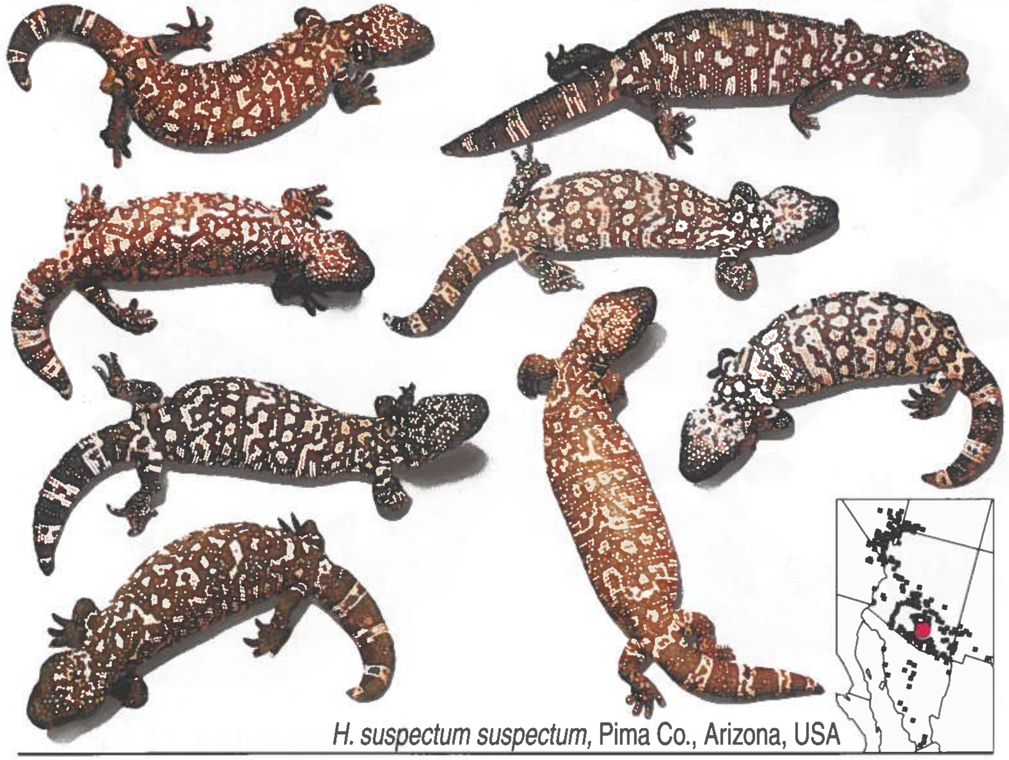
H. suspectum cinctum, Washington Co., Utah, USA



H. suspectum cinctum, Clark Co., Nevada, USA

PLATE 15. Portraits of populations: These photographs show a typical range in variation of dorsal patterns within populations of *Heloderma suspectum cinctum*, the Banded Gila Monster. Notice the darker, nonbanded morph found in southwestern Utah, a region near the northern periphery of the range where only lighter-colored, banded adults were previously thought to occur.

H. suspectum suspectum, Maricopa Co., Arizona, USA

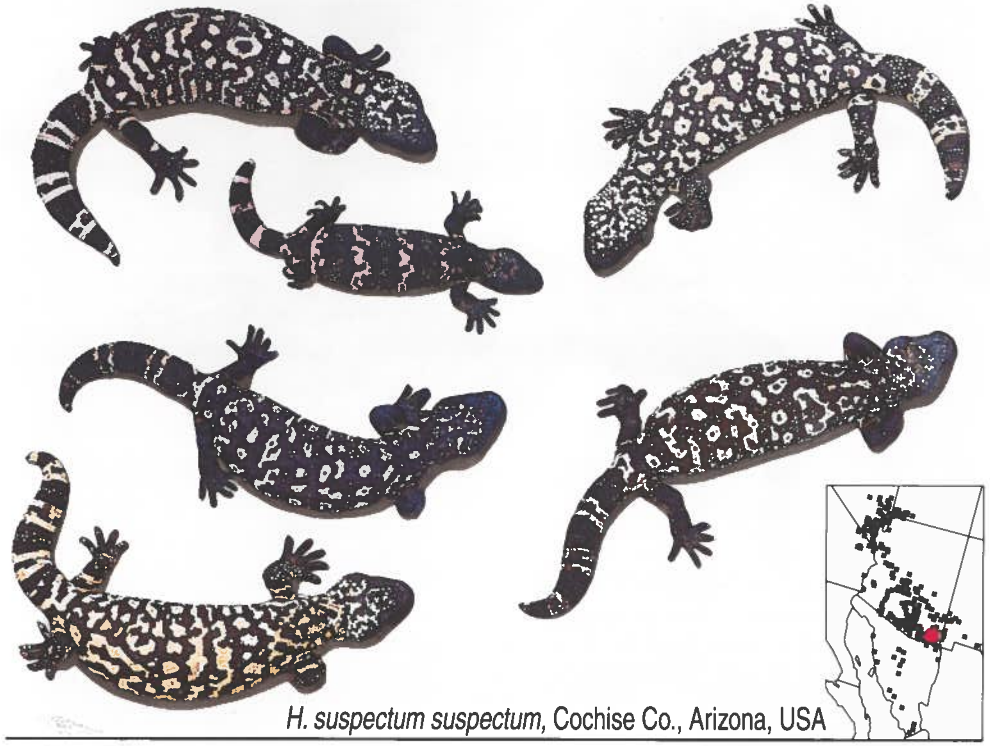


H. suspectum suspectum, Pima Co., Arizona, USA

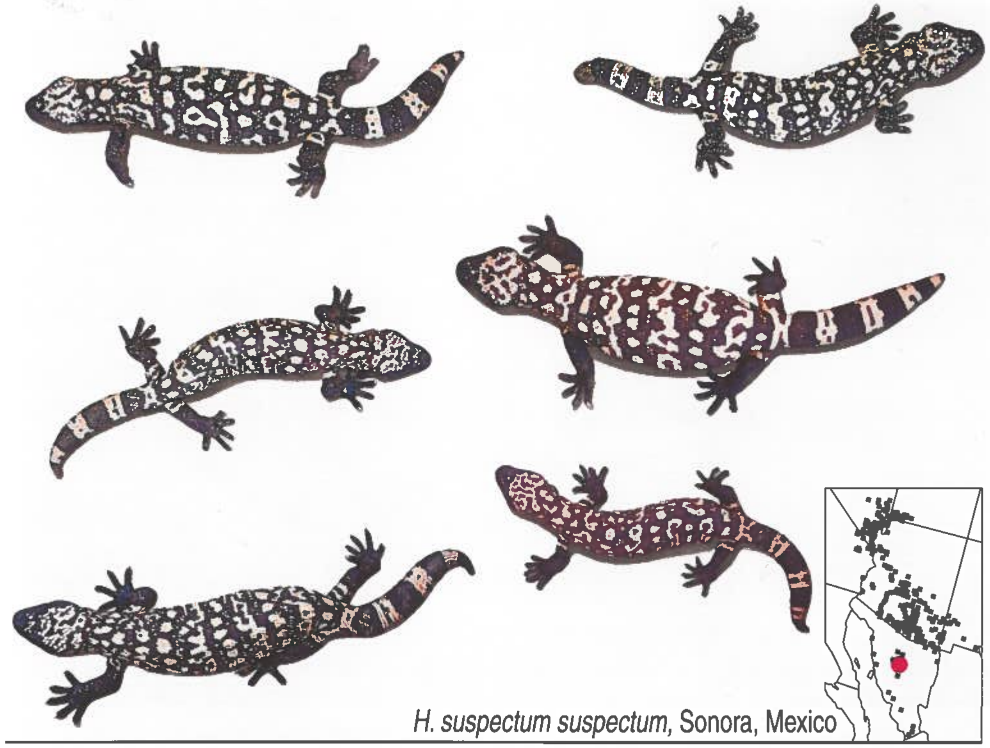
PLATE 16. Portraits of populations: These photographs show a typical range in variation of dorsal patterns within populations of *Heloderma suspectum suspectum*, the Reticulate Gila Monster. Individuals from Maricopa Co., AZ (top), near where the "reticulate" and "banded" morphs are thought to intergrade, more commonly show banding. Individuals from Pima Co., AZ (bottom), clearly show reticulate patterns.

H. suspectum suspectum, Grant Co., New Mexico, USA

PLATE 17. Portraits of populations: These photographs show a typical variation of dorsal patterns within a population of *Heloderma suspectum suspectum* near Redrock, NM, in the heart of the range of the Reticulate Gila Monster. Notice how many individuals from this population show the lighter, banded pattern characteristic of *H. s. cinctum* populations to the north.



H. suspectum suspectum, Cochise Co., Arizona, USA



H. suspectum suspectum, Sonora, Mexico

PLATE 18. Portraits of populations: These photographs show a typical range in variation of dorsal patterns within populations of *Heloderma suspectum suspectum* from Cochise Co., AZ, and Hermosillo, Sonora, near the southern extent of their geographic distribution. Notice how these individuals are consistently darker and adults show little sign of the banded juvenile pattern.

PLATE 19. Hatchling Gila Monsters can be confused with adult Banded Geckos *(Coleonyx variegatus)*, which occur in many of the same habitats as Gila Monsters. The smaller, thinner gecko is easily distinguished by its velvety skin, vertical pupils, and more slender head, among many other features.

PLATE 20. The venom glands in this Gila Monster are visible as conspicuous bulges in its lower jaw. Rare bites to humans — almost always the result of harassment or careless handling — are not deadly. However, the venom contains a number of lethal toxins that cause hypotension, inflammation, and pain that may be excruciating enough for an adversary to consider death the preferred alternative. For a lizard that cannot skitter out of harm's way, the utility of such a defensive venom system is obvious.

PLATE 21. Helodermatid lizards store fat in their sausage-shaped tails, which make their trails in sandy habitats easy to identify. Stored energy is used very slowly, an important asset for a lizard that might need to go a year without feeding, as occurs in some of its harshest habitats, like this sandy desert in southern Nevada.

PLATE 22. The Chiapan (or Río Grijalva) Beaded Lizard, *Heloderma horridum alvarezi*, inhabits tropical dry forests in the valley of Río Grijalva, shown in this wet-season photo coursing through the Canyon Sumidero east of Tuxtla Gutiérrez, Chiapas.

PLATE 23. The striking seasonal changes of tropical deciduous forests inhabited by *Heloderma horridum* are shown in these photographs taken during the dry season (top) and wet season (bottom) near Alamos, Sonora (photos by Jack Dykinga).

PLATE 24. *Heloderma suspectum* in Arizona upland habitat of the Sonoran Desert near Tucson, AZ.

PLATE 25. Semidesert grassland/Chihuahuan Desert habitat of *Heloderma suspectum suspectum* near Redrock, NM (photo by D. Beck).

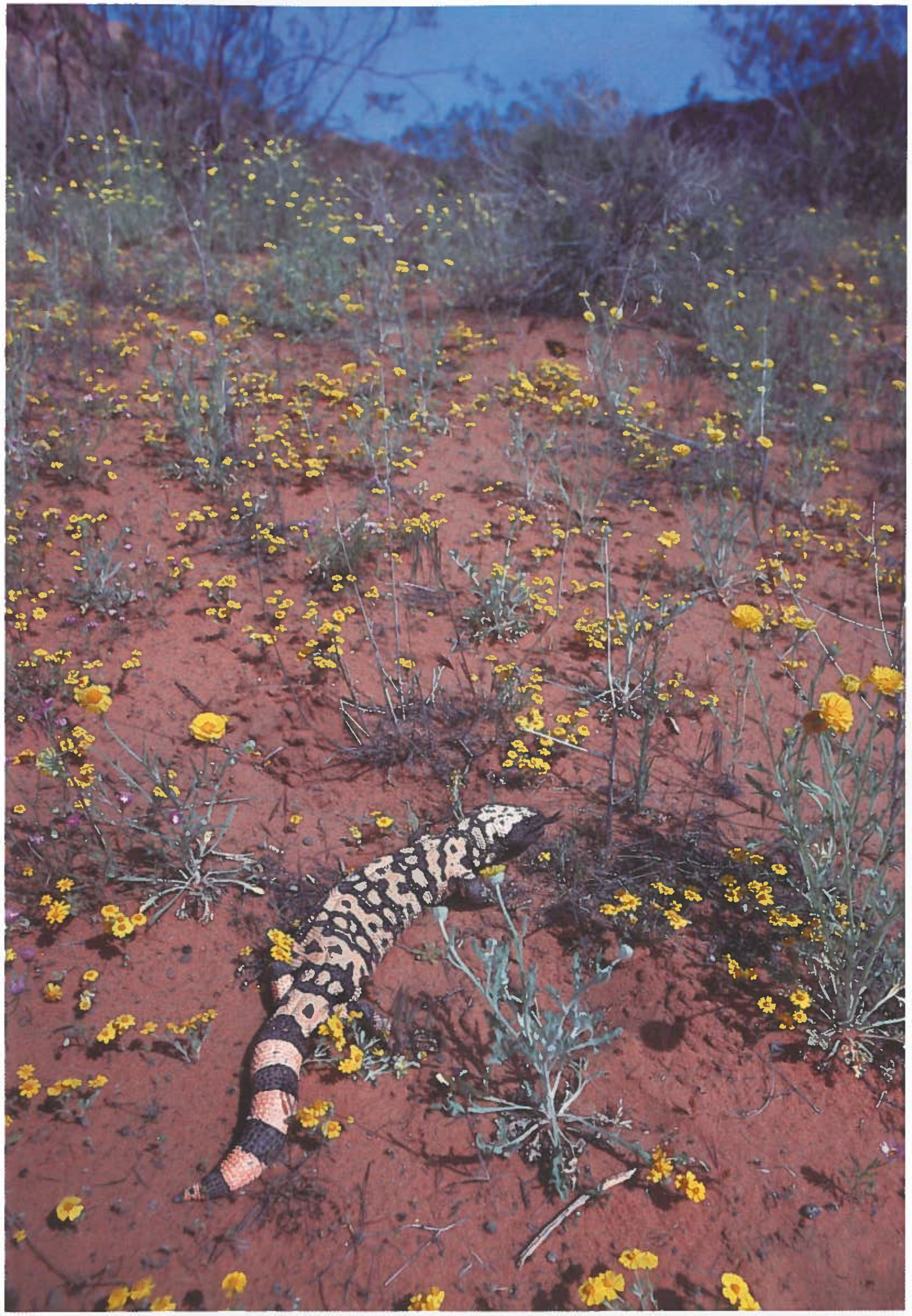


PLATE 26. A *Heloderma suspectum cinctum* exploring its Mohave Desert habitat in Paradise Canyon, UT (photo by D. Beck).

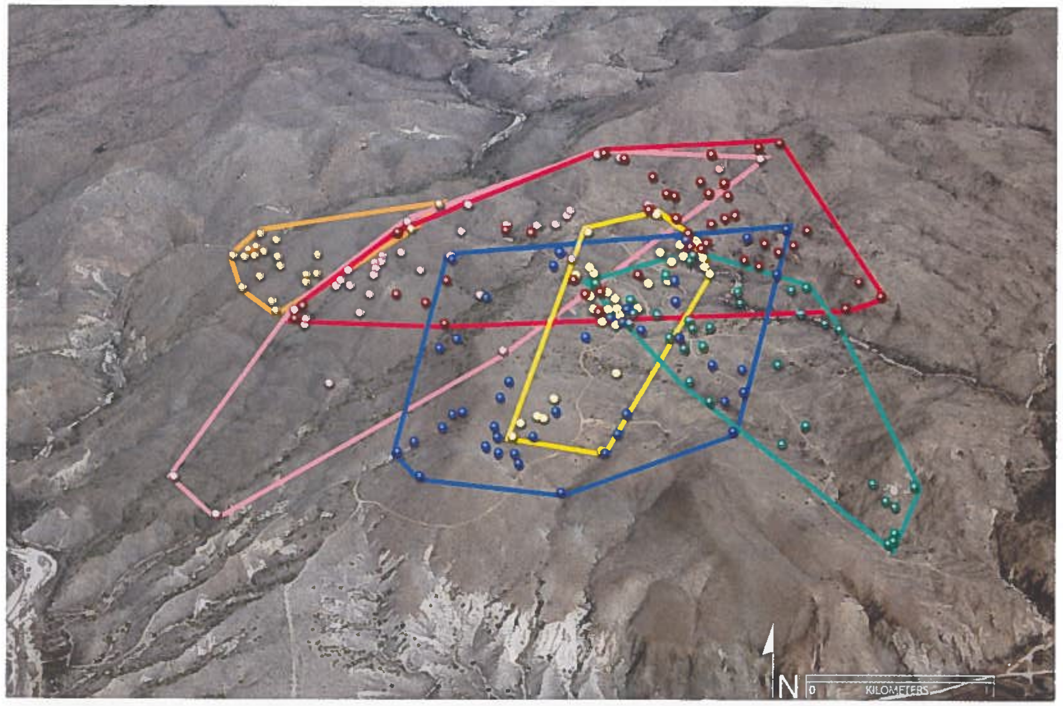


PLATE 27. Shelter site locations (dots) used by six Gila Monsters in southwestern New Mexico between November 1992 and June 2000. Each color denotes an individual Gila Monster (red, green, and blue = males; yellow, orange, and pink = females). Minimum convex polygon home ranges are indicated by solid lines (see also table 13).

LATE 28. Although the majority of their foraging activity takes place on the forest floor, Beaded Lizards commonly climb up o between 5 and 7 m into trees where they search for nests and use hollow trunks and branches as shelters.

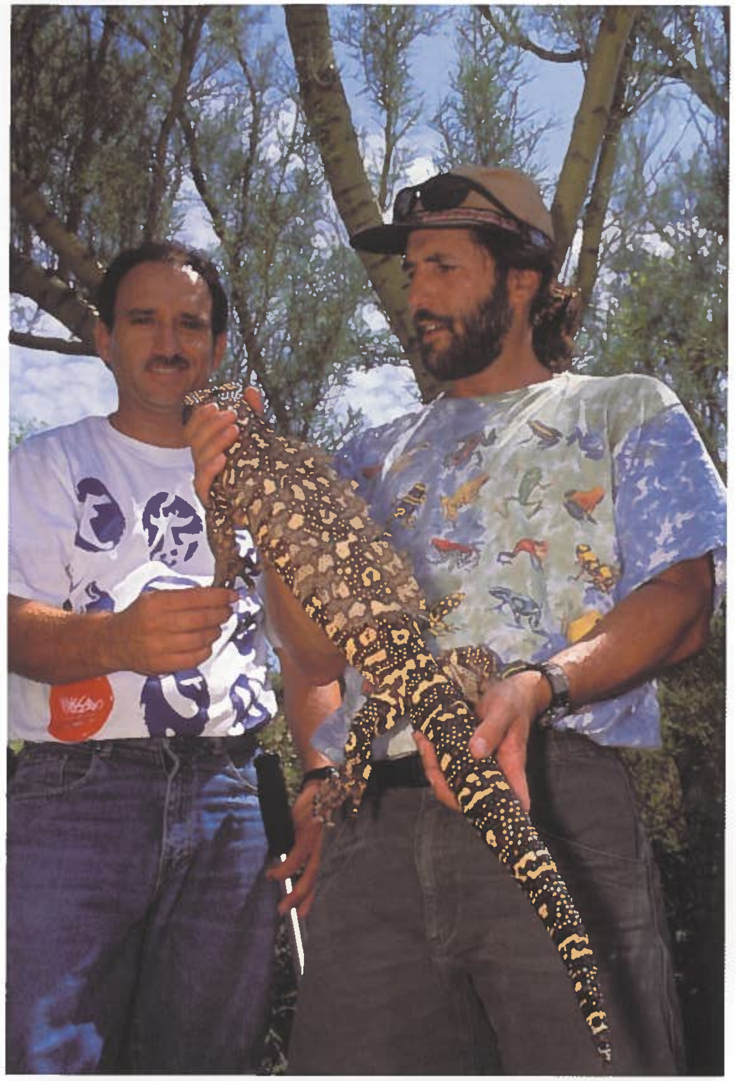


PLATE 29. Martín Villa, from Centro de Ecología de Sonora, with the author holding a near-record-size Río Fuerte Beaded Lizard, *H. horridum exasperatum*.

PLATE 30. Snakes are important predators on helodermatid lizards. The last of a juvenile *H. suspectum suspectum* is swallowed by a California King Snake, *Lampropeltis getula*, in a rare glimpse of predation in the Sonoran Desert of southern Arizona (photograph courtesy of Matt Goode).

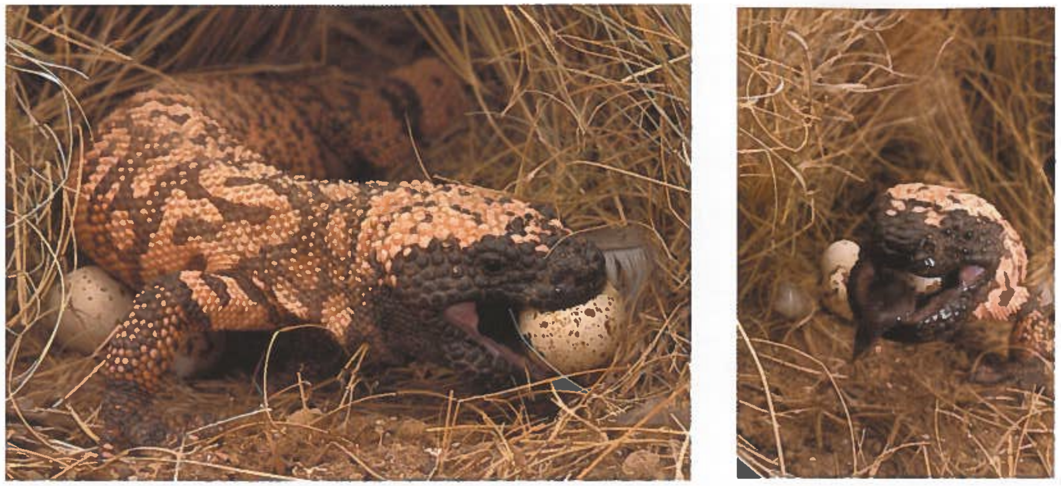


PLATE 31. When Gila Monsters and Beaded Lizards feed on eggs—as on the quail eggs shown here—they often take the entire egg into their mouth, then partially crush it before swallowing. In contrast to many other lizard groups, *Heloderma* use their jaws—rather than the tongue—to engulf prey. This frees the tongue to be used primarily as a chemosensory organ, an evolutionary step believed to have resulted in the amazing specialization of the forked tongue for finding hidden prey, found in nests (seen here).

PLATE 32. Typical posture shown by mating Gila Monsters: male is at bottom of drawing, with leg hooked over base of female's tail. Such a revealing view of mating, occasionally seen in captive Gila Monsters, has never been observed in nature because it takes place within the privacy of shelters (color drawing by Randy Babb from photographs provided courtesy of Mark Seward).

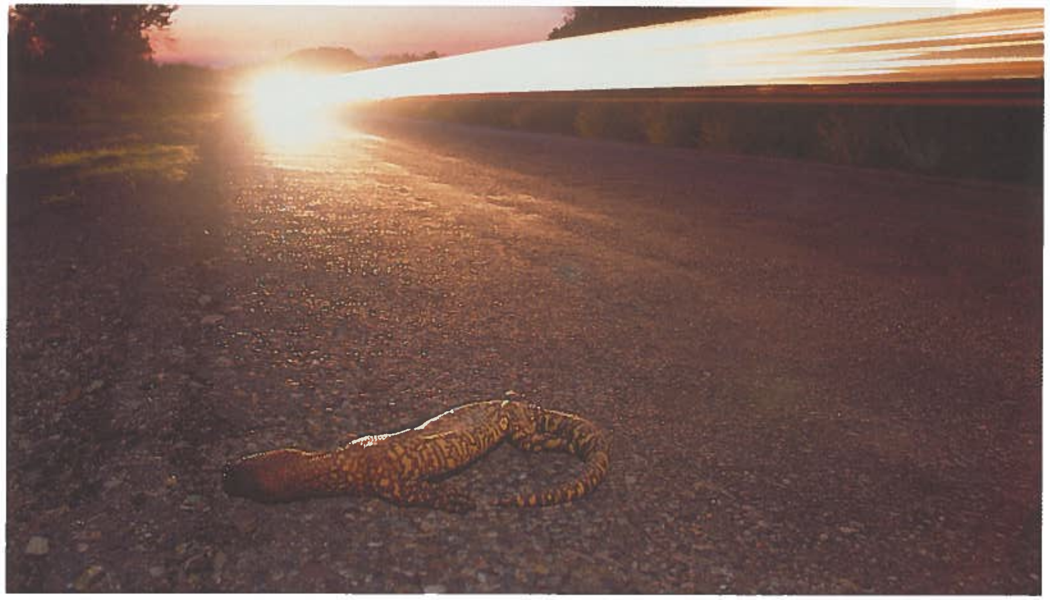


PLATE 33. An untold number of Beaded Lizards and Gila Monsters, including this *H. horridum exasperatum* lying dead on the road to Alamos, Sonora, are killed each year on an increasing number of paved roads that penetrate their habitats.

PLATE 34. Although a capable swimmer, a Gila Monster in a suburban pool is like a fish out of water. Each year, numerous homeowners in suburban areas of the southwestern United States report Gila Monsters falling into swimming pools, or venturing into garages, porches, utility rooms, backyards, patios, and even bedrooms. A disoriented Gila Monster in a swimming pool can easily be scooped from the water with a net and placed back into the surrounding desert.

PLATE 35. Antonio Ramírez, a herpetologist at Zoo Miguel Álvarez del Toro (ZooMAT) in Tuxtla Gutiérrez, Chiapas, explains to a group of children what makes this animal, the Río Grijalva Beaded Lizard *(H. h. alvarezi)*, so special. ZooMAT offers an engaging environmental education program that is helping citizens develop an appreciation of the rich biodiversity of southern Mexico.

free-ranging Gila Monsters averaged 165 mm in total length and weighed, on average, 33 g.

Captive-born Gila Monsters emerge with a SVL of 115 mm, a tail length of 46 mm, and weighing 28–36 g (Shaw 1968; M. Seward, pers. comm.) Ramírez-Bautista (1994) reports finding 6 hatchlings of *H. horridum* in July, ranging in mass from 23–27 g and 115–127 mm in SVL. Captive-raised *H. horridum* hatchlings range in mass from 38 to 47 g (Conners 1987; Applegate 1991; Gonzales-Ruiz et al. 1996). Keepers at the San Diego Zoo have successfully reproduced Guatemalan Beaded Lizards, *H. h. charlesbogerti* (Owens et al. 2003). Four eggs hatched from a clutch of 10 laid from December 7 to December 17, 2002. The incubation period was 145 to 148 days at incubation temperatures of 30°C (86°F). The hatchlings ranged in SVL from 119 to 123 mm (197–208 mm in total length) and weighed 33.5 to 36.9 g.

Observations of hatching in captive *Heloderma* suggest that they use an egg tooth to slit the shell, although in some cases hatchlings are born without an obvious egg tooth (Anstandig 1984). There is also evidence that hatchlings may use their clawed toes to at least partially break out of the egg (fig. 54).

At hatching, over 50% of the egg mass may be yolk yet to be absorbed (Shaw 1968). As the hatchling emerges from the egg, it absorbs this yolk, which becomes an important energy source for the first several weeks of life. This large quantity of yolk absorbed by hatchlings may even distend their abdomens, making it difficult for them to emerge from the egg (Shaw 1968; plate 10). The process of yolk absorption may take several days; Gila Monsters remain within the opened eggshell during that time and may die if removed prematurely (Strimple 1995).

Hatchling Gila Monsters get their first taste of egg very early. Upon emerging from the egg, they may turn and lap up any remaining liquid within their own now-vacant egg (J. Branham and M. Seward, pers. comm.). Hatchlings even visit other empty eggs in a clutch and continue lapping until all eggshells are dry (M. Seward, pers. comm.). Hatchling *Heloderma* emerge immediately prepared to defend themselves and readily open their mouths, hiss, and attempt to bite. The coloration of newborn *Heloderma* is a strongly banded, striking black-and-white pattern. Pink, yellow, or orange coloration does not appear until after a few months of age.

After hatching, Gila Monsters may remain in or near the nest for weeks, even months. Why don't hatchling *Heloderma* emerge to forage earlier in spring as do adults? One explanation may be that hatchlings are largely nocturnal. The vast majority of observations of juvenile and hatchling Gila Monsters occur at night. Throughout the range of *H. suspectum*, nights are too cold until late April or early May to permit maintenance of body temperatures above approximately 25°C. In addition, nocturnal activity reduces the risk both of predation and of dehydration through excessive evaporative water loss. Moreover, an important part of the diet of juvenile Gila Monsters appears to be lizard eggs (chap. 7), and most lizards sympatric with *H. suspectum* (with the exception of *Uta stansburiana*) do not lay eggs until May or later.

HELODERMA IN CAPTIVITY

Beaded Lizards and Gila Monsters are beautiful animals, but they are venomous and potentially very dangerous. They should never be collected from the wild and kept as pets. For one, collecting a wild *Heloderma* is against the law unless valid collecting and transport permits are obtained. Under the Lacey Act, it is a federal crime to "import, export, transport, sell, receive, acquire, or purchase" any wildlife, alive or dead, that was obtained in violation of any state or Indian law or regulation. Both species of *Heloderma* receive full legal protection throughout every state (and country) where they occur. In addition, keeping a venomous animal as a pet is risky. The extremely painful venomous bite of a helodermatid lizard is a serious medical emergency that may be life threatening in small children. Nearly all bites occur from careless handling of captive animals, and some put their owners in the hospital (chap. 3).

CHAPTER 9

Conservation

THROUGHOUT MUCH OF their range, helodermatid lizards inhabit only a fraction of what was once suitable habitat. During the past 150 years, thousands of square miles of desert and tropical dry forest habitats have been cleared for agriculture, housing, and recreational development. On the other hand, much suitable habitat still remains for *Heloderma*. Open tracts of desert habitat occur in Arizona both on state and federal lands within national parks and monuments and in federal wilderness areas. In western Mexico, vast regions of tropical dry forest still remain, although these are rapidly disappearing (see below). Mexican Beaded Lizards and Gila Monsters are not in jeopardy of rangewide extinction.

However, this encouraging situation should not invite complacency. A major threat to *Heloderma* populations today continues to be loss and degradation of their remaining habitats, especially along the edges of their geographic distributions. *Heloderma* is one of the most commercially valuable reptiles in the world, and, even though extensive laws protect them throughout their range, poaching and illegal commerce also pose a significant threat. *Heloderma* are long-lived and have a relatively low reproductive potential and an ability to endure long periods of food shortage. Therefore, barring a catastrophic disease outbreak, such as that which struck the Desert Tortoise and placed it on the U.S. endangered species list (see below), it may take many years for the cumulative effects of habitat loss and degradation to be seen on afflicted *Heloderma* populations. Yet, because so few baseline data exist, it will be difficult to know the threshold below which rangewide declines in *Heloderma* populations would threaten their existence. Some populations, such as those in southwestern Utah and Guatemala, are already in jeopardy.

This suggests that a proactive approach is imperative for conservation of helodermatid lizards. It will be far more difficult for *Heloderma* populations to recover, if they can recover at all, if we wait until they are on the endangered species list or near the brink of extirpation before management agencies take action to identify and preserve habitats sufficient for maintaining viable and sustainable populations. Because large tracts of suitable habitat still exist, we have a priceless opportunity to wisely manage remaining habitat so that *Heloderma*, and the many species that share their habitat, will persist into the foreseeable future.

In this chapter, I'll provide an overview of the conservation biology of Gila Monsters and Beaded Lizards. I'll outline the threats to helodermatid lizards and explain their legal conservation status. Finally, I'll discuss some conservation strategies for what I hope can develop into an agenda for protecting these lizards, and their habitats, for future generations.

THREATS TO HELODERMATID LIZARDS

HABITAT LOSS AND ALTERATION

Habitat loss takes many forms, from direct clearing or conversion of former habitat for human use to more subtle changes that result from the cumulative effects of agriculture, development, recreation, invasive plants, fire, livestock grazing, motorized vehicles, and pets. Not enough is known about the historic patterns of distribution and abundance of helodermatid lizards to quantify specific population losses that are attributable to these broad landscape-level changes in habitat quality. However, many of the consequences of habitat loss and alteration are well known.

FRAGMENTATION AND DEGRADATION

When an area is converted from desert or dry forest habitat into an agricultural field or a housing development, for example, patches of previously connected habitats become separated from others. Roads may add additional barriers that isolate populations and contribute to habitat fragmentation. Immigration, emigration, and gene flow among once-connected populations greatly slows or comes to a halt. To persist, remaining populations must now not only rely on a smaller resource pool within a smaller area, but also contain reduced genetic variability and recruitment within their separated habitat patches. These smaller, separated populations, therefore, generally have lower absolute rates of recruitment, reduced genetic variability, and higher risks of extinction (Petterson 1985; Noss and Csuti 1997).

Habitat fragmentation generally leads to a population less able to tolerate extreme events such as energy shortages associated with occasionally severe drought. There are certain traits, such as rarity, low fecundity, and vulnerability to human persecution/exploitation (among others), that make some species more susceptible than others to local extinction when habitats become fragmented (Rabinowitz 1981; Noss and Csuti 1997). Rare species (i.e., those with limited or patchy geographic distributions, low population densities, or both) are particularly vulnerable to habitat fragmentation. Helodermatid lizards seldom attain high population densities and have only moderate reproductive potentials (chap. 6). In addition, both species of *Heloderma* are vulnerable to commercial exploitation and human persecution (see below). For these reasons, helodermatid lizards may be particularly susceptible to habitat fragmentation.

Isolated or fragmented populations are also more vulnerable to further habitat degradation caused by edge effects, invasion of nonnative species, predators, and disease. Edge effect refers to the negative influence that a habitat edge may have on conditions, or species, within the interior of the habitat. For example, habitat along the edge of a housing development or agricultural field may be more vulnerable to invasion by exotic, weedy species such as bromegrass (which is a major contributor to habitat degradation in the American Southwest; see below). Almost all of *Heloderma*'s prey species are primary consumers (herbivores) that depend on the ecological integrity of native plant communities (golf courses excluded). If such herbivorous prey species are reduced, so too will *Heloderma* populations be negatively affected. In many of the suburban developments of the southwestern United States, Gila Monsters active along edge habitats may also be more vulnerable to mortality from marauding domestic cats and dogs (see below). Domestic dogs and cats also kill prey species of Gila Monsters (e.g., cottontail rabbits, squirrels, quail), which may, in turn, reduce the prey base available to foraging Gila Monsters. Lizards that venture beyond habitat edges into human developments are at even greater risk of mortality from cars or people, or removal from the population (see below), which may take a heavy toll on population densities within the core habitat. For helodermatid lizards, one can only speculate on these edge effects because they have not yet been investigated directly.

In some cases, small-scale edge habitats may be beneficial to helodermatid lizards. Spiny-tailed Iguanas *(Ctenosaura pectinata)* often lay their eggs in sandy soils along the boundaries of small agricultural fields adjacent to tropical dry forest habitats. More sunlight reaches these open areas than the more closed understory of denser forest. The enhanced thermal options of such edge habitats may provide better nest sites for Spiny-tailed Iguanas, an important food item for *H. horridum*.

Because helodermatid lizards depend greatly on microhabitat features such as crevices, boulders, burrows, and pack rat middens for shelters (see chap. 5), subtle disturbances to their microphysical environments could have negative effects. Gila Monsters spend more time in areas that contain a higher density of potential shelters, and they select shelters based on rockiness, entrance aspect, depth, humidity, and temperature (Beck and Jennings 2003). Disturbances that alter the availability or suitability of shelters (such as erosion, alteration of shrubs that stabilize soil burrows, off-road vehicle use, or the collapsing of burrows by horses, hikers, or mountain bikers) could degrade Gila Monster habitat. Box turtle populations suffer from alterations to their biophysical environments brought about by habitat fragmentation, even when habitat patches are sufficiently large to theoretically sustain viable populations (Curtin 1997). Apparently, subtle changes in box turtle microenvironments result in greater movements within their home ranges, longer egg-incubation periods, increased mortality, and decreased recruitment (Curtin 1997). In addition, subtle changes in the soil microenvironment could have negative effects on nests, about which we know very little for *Heloderma*. Evidence from our New Mexico study (see chap. 8) suggests that nests may be placed in or near soil burrows, sites that may differ markedly from those used during other periods. Subtle temperature and moisture requirements of eggs and developing embryos may be important in limiting the distribution and persistence of helodermatid lizard populations.

INVASIVE PLANTS AND FIRE

In deserts of North America, nonnative invasive plants have become one of the greatest threats both to the integrity of native habitats and to the animal species they harbor (Brooks and Pyke 2001; Brooks and Esque 2002). Invasive plants may outcompete native plant species, alter wildlife habitat, and promote fire, erosion, and further invasion by exotics in desert habitats where fire was historically infrequent. For *Heloderma*, perhaps the biggest problem in the Sonoran Desert is invasion by alien grasses, such as the annual red brome *(Bromus rubens)* from the Mediterranean and perennial buffel grass *(Pennisetum ciliare)* from Africa. In tropical dry forest habitats of *H. horridum*, buffel grass also is increasing at an alarming rate (Martin and Yetman 2000). These grasses provide a dense conduit of highly flammable vegetation between desert shrubs and subtrees where once there was little connection. After periods of rain these nonnative grasses may grow much more densely and profusely than native grasses, and they greatly increase the fuel load to a system that rarely experiences fire. Once the habitat burns, many native species are destroyed (saguaros and paloverdes are readily killed by fire) and the habitat becomes increasingly prone to burning again (D'Antonio and Vitousek 1992; Esque et al. 2002). Habitat structure is also severely altered as life-forms such as succulents and subtrees are replaced by grasses. Microhabitats are in turn altered as plant life-forms (and the microclimates associated with them) become more homogeneous. One disturbing fact is that some exotic species even colonize relatively pristine native habitats, far removed from developed areas.

Habitat conversion brought about by invasive plants and fire has had severe negative effects on Desert Tortoise habitat in the Sonoran and Mohave deserts (Brooks and Esque 2002; Esque et al. 2002, 2003). Individuals are either killed directly, or their long-term fitness is compromised as the plants and microhabitats on which they depend are altered by fires. *Heloderma* populations may be affected in similar ways (Esque et al. 2003).

HABITAT THREATS AND HUMAN POPULATION GROWTH

How immediate and how widespread are these effects of habitat alteration on helodermatid lizards? Habitat loss and degradation are a menace to *Heloderma* populations throughout their range, but the biggest threats are found along the margins of their distribution, where populations tend to be patchy and human populations are expanding exponentially. In the northern Mohave Desert of southern Nevada and California, the U.S. Fish and Wildlife Service (FWS) listed the Gila Monster as a high-priority species. In outlining management needs, FWS biologists wrote: "As the rate of human encroachment into the desert habitats of Nevada and southeastern California continues to increase, our knowledge of the effects of this encroachment or even the status of the resident species potentially impacted by this encroachment lags far behind. The . . . [Gila Monster] . . . is believed to be at serious risk, but so little is known of its status and basic biology that the steps needed to preclude ESA [Endangered Species Act] listing are unknown." Clark County, Nevada, where the vast majority of Gila Monster records occur in that state, is the fastest-growing county in the United States, and the Las Vegas Valley (within Clark County) has been one of the fastest-growing suburban areas in the United States for many years (U.S. Census Bureau 2002). However, there is not sufficient information on the occurrence of Gila Monster populations in or around the Las Vegas Valley, or of historical trends, to conclude that the enormous growth of Las Vegas has contributed to the decline of the Gila Monster in Nevada. Gila Monster populations still exist in Nevada outside the direct path of current development (Gienger 2003).

In California, Gila Monster populations appear to be extremely rare and, therefore, vulnerable to habitat destruction. They are restricted to only a few isolated mountain ranges in the Mohave Desert, most of which are owned by the U.S. Bureau of Land Management or private mining companies, areas that appear to be secure from immediate development.

A more ominous situation exists in the Mohave Desert of southwestern Utah. The majority of Gila Monster populations have already been lost from that state, and most remaining populations are in the direct path of another of the nation's fastest-growing communities. Gila Monsters occur in Utah solely within Washington County, the fourth-fastest-growing county in the United States. From 1980 to 1990, Washington County's human population nearly quadrupled in size, from 26,125 to over 90,000, excluding the estimated 20,000 temporary resident "snowbirds" who add to the population each winter (Washington County Water Conservancy District 1991; U.S. Census Bureau 2000). Estimates for 2005 tip the county's population over 100,000. Historically, the best Gila Monster habitat in Washington County surrounded the town of St. George, just southwest of Zion National Park. In the 20 years between 1980 and 2000, St. George saw its population increase nearly 438%, from 11,350 people in 1980 to 49,663 in 2000 (U.S. Census Bureau 2000). Estimates for 2005 place the population at 60,000. This once-tiny farming community has grown into a bustling hub of recreation and real estate development and surrounding cities have followed suit, swallowing most of the Gila Monster habitat that once existed in southwestern Utah.

Most prime Gila Monster habit in Utah occurs in a broad arch north of the community of St. George, directly in the path of rapidly expanding housing and recreational developments (plate 12). Gila Monster populations are at their elevational and latitudinal limits in this region; as recreational growth continues to expand northward, displaced populations have nowhere to go. Paradise Canyon, named in the 1970s by Eric Coombs because of its plethora of Mohave Desert reptiles, once contained the most robust populations of Gila Monsters, Chuckwallas, Sidewinders, and Desert Tortoises known in Utah (Coombs 1977; Beck and Coombs 1984; Beck 1985b, 1990). Today, the southern end of Paradise Canyon has been converted to a housing development and apparently few tortoises or Gila Monsters remain, despite the fact that the Desert Tortoise has been federally listed as a threatened species, and great efforts have gone into setting aside habitat in Utah for its protection (see below). Clearly, significant conservation efforts must be taken if viable *H. suspectum* populations are to persist in Utah.

Arizona, the heartland of Gila Monster habitat, is also experiencing rapid growth. Hundreds of Gila Monsters are killed or displaced each year because of the expanding urban and rural development of cities such as Phoenix and Tucson (D. E. Brown and Carmony 1991). Concrete-lined canals may present barriers to movement and further fragment their habitat. There are still hundreds of square miles of suitable habitat remaining for *Heloderma* in Arizona on public lands in national parks, national monuments, wilderness areas, and other Sonoran Desert ecosystems protected from habitat conversion. Although this situation provides hope for the future, it should not invite complacency. Instead, it presents an opportunity to wisely manage existing habitats in Arizona before Gila Monster populations become threatened (see Conservation Strategies, below).

HELODERMA HORRIDUM AND TROPICAL DRY FOREST

Throughout its range, the Beaded Lizard occurs almost exclusively within or adjacent to tropical dry forest habitats (TDF; see chap. 5). Tropical dry forests, not rain forests, hold the distinction of being the most threatened of the earth's major forest types (Janzen 1988a). When the Spaniards arrived in the Western Hemisphere, neotropical dry forest covered a region stretching from Panama north to western Mexico, roughly the size of France (~550,000 square kilometers). Today, only 0.09% of that region (480 km^2) has official conservation status, and less than 2% remains sufficiently intact to attract the attention of conservationists (Janzen 1988a). Even though tropical dry forests are less rich than tropical rain forests in total species diversity, dry forests are much richer in their diversity of species *activities,* such as their numerous adaptations to seasonal drought, plant growth forms, and insect parasitoid strategies (Janzen 1988a). And although large tracts of tropical rain forest still remain today (albeit under siege), most of the tropical dry forests that once existed were converted to agriculture by the early twentieth century (Janzen 1988a).

Some of the earth's largest remaining tropical dry forests are those of western Mexico (Ceballos and Garcia 1995), which harbor the vast majority of *H. horridum* populations. Mexico is considered a country of "megadiversity," containing around 10% of the earth's known biota, and tropical dry forests are among the richest of its ecosystems (Ceballos and Garcia 1995). These forests have been largely isolated—geographically and ecologically—from other tropical forests, a process that has apparently contributed to a great number of endemic vertebrate species in the TDF of western Mexico (Ceballos 1995). For reptiles and amphibians, 173 species (43%) are restricted to the tropical dry forests of western Mexico (García-Aguayo and Ceballos 1994; Ceballos 1995). In Mexico, CONABIO (Comisión Nacional para el Conocimiento y Uso de la Biodiversidad) has identified several tropical dry forest sites to be protected from conversion (García-Aguayo 2003). Many of the locality records for both species of *Heloderma,* unfortunately, fall outside the boundaries of these proposed protected areas (fig. 55).

At the southern edge of *Heloderma*'s geographic range, in the Motagua Valley of eastern Guatemala, populations of *H. horridum charlesbogerti* appear particularly vulnerable (Ariano Sánchez 2003). Since this subspecies was first described (Campbell and Vannini 1988), habitat for *H. h. charlesbogerti* has undergone considerable change. Most of the Motagua Valley floor has been subjected to irrigated agriculture (cantaloupe, tobacco, etc.), and many of the hillsides have been stripped of the original vegetation and are often planted with corn (although the area is so dry that corn crops regularly fail [J. Campbell, pers. comm.]). There are a few

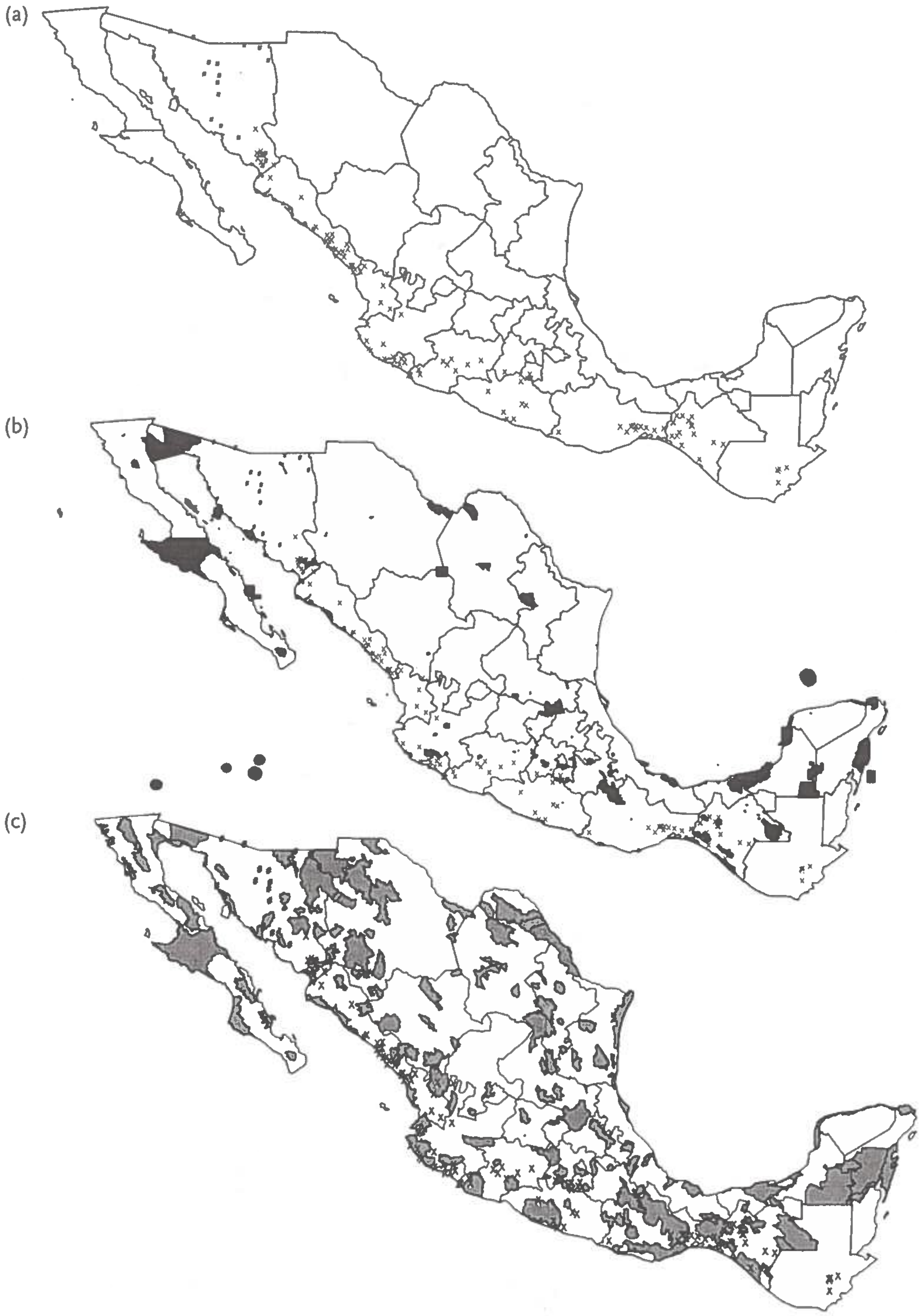


FIGURE 55. Maps showing (A) distribution of *Heloderma* in Mexico (x = *horridum;* # = *suspectum*), (B) areas protected in national parks and reserves as of 2003, and (C) proposed areas to be protected by CONABIO. Note that even with significant added habitat protection, most of the records for *Heloderma* fall outside the boundaries of protected areas (maps courtesy Andrés García-Aguayo).

slopes where rocky outcroppings and original dry forest persists, but the extent to which these harbor suitable habitat for *H. h. charlesbogerti* is poorly known. *Heloderma* in Guatemala have been extirpated from more than half of their original area, perhaps considerably more (J. Campbell, pers. comm.). Overall, the populations are reduced and in sad shape as compared with the situation a few decades ago. Remaining populations continue to persist, however, in a few of the rockiest, most remote areas.

The primary threats to remaining TDF include wide-scale clearing for agriculture and development, and exotic grasses, such as buffel grass, which often accompany such habitat conversion. In some tropical dry forest habitats, such as those of southern Sonora, local cultures have maintained small-scale, sustainable forestry, farming, and ranching operations since early colonial times (P. S. Martin and Yetman 2000). Crops, such as corn planted in small fields or milpas, were frequently grown in small forest clearings that quickly regenerated to forest as fields were abandoned. Many trees and shrubs that provide wood for folk art, furniture, and farm implements have been continually harvested for generations by people inhabiting Mexican tropical dry forests (P. S. Martin and Yetman 2000).

Today, however, socioeconomic pressures have squeezed out these smaller farming and ranching operations and are continuing to remove large tracts of remaining tropical dry forest habitats and replace them with buffel grass used to support high-production cattle ranches. Some of these large ranches in southern Sonora are also believed to be used for laundering money produced by the illegal drug trade (P. S. Martin and Yetman 2000). Tracts of dry forest habitat are acquired by "narcotraficantes" (who have considerable disposable income), cleared, and replaced with buffel grass along with as many cattle as possible. Such "ranches" are a convenient means of accounting for large incomes and expenditures that might otherwise be difficult to explain (P. S. Martin and Yetman 2000). Tropical dry forests have yet to be used as a major source of lumber, although many tropical dry forest trees such as *Cordia* spp., *Enterolobium* spp., and *Dalbergia* spp. are in high demand in the exotic lumber industry.

The high demand for tequila has also put some Mexican tropical dry forests at risk (plate 11). These forests harbor a plethora of readily available agave plants, or maguey, used to make tequila. A sudden rise in demand during the late 1990s led tequila manufacturers to strip Mexican tropical dry forests in an effort to quickly harvest agave plants and satisfy the demand for this intoxicating drink.

DIRECT HUMAN-CAUSED MORTALITY

Aside from habitat loss, humans contribute to the mortality of helodermatid lizards in four general ways. Lizards are killed wantonly by people because of ignorance and fear, as a result of displacement, by domestic pets (cats and dogs), and by automobiles (plate 33). At one time, Gila Monsters were routinely killed when encountered by humans, simply because they were venomous and believed to be dangerous. Even today some homeowners who seek to remove "undesirable" life-forms from their immediate surroundings may kill Gila Monsters without knowing, or in some cases without caring, that it is against the law. Because they are relatively slow moving, once a Gila Monster or Beaded Lizard is spotted by a person, the lizard becomes easy prey. As late as the turn of the twenty-first century, people were observed, or heard boasting of, shooting or beating Gila Monsters to death (D. E. Brown and Carmony 1991; Degenhardt et al. 1996). Such wanton killing is no longer the rule in the United States, but in Mexico many still view the Beaded Lizard, or escorpión, as loathsome and dangerous, and many Beaded Lizards encountered by farmers and ranchers are regularly killed (Ariano Sánchez 2003). On the other hand, increasing numbers of people who live and work in Beaded Lizard habitat now view the animals with respect and avoid killing them (plate 35).

In suburban areas in the southwestern United States, Gila Monsters commonly fall into swimming pools (plate 34) and venture into garages, porches, utility rooms, backyards, patios, and even bedrooms (table 22). In 2001 alone, 196 Gila Monsters were reported to the Rural–Metro Fire Department by homeowners in the foothills of the Catalina Mountains around Tucson, Arizona (fig. 56). Some homeowners may enjoy an encounter with such a rare, unique visitor, and simply allow the lizard to continue on its way. Others, who feel uncomfortable with a venomous reptile in their midst, may request that the fire department remove the animal from the premises. Over the years, a common solution for dealing with such "nuisance" Gila Monsters has been to capture the lizard and release it into a locality away from human habitation with the hope that the Gila Monster would settle into a new territory and not further disturb people. This has long been a common practice for dealing with other venomous reptiles as well, such as rattlesnakes (Hare and McNally 1997; Nowak et al. 2002). Hundreds of Gila Monsters in suburban areas such as Phoenix, Tucson, and St. George have been displaced in such a manner by the development boom occurring in the Southwest over the past several decades. Unfortunately, relocated "nuisance" Gila Monsters may show greatly decreased survivorship (Sullivan et al. 2004), and such displacement might be more accurately described as a form of mortality than a conservation strategy (see below). Many Gila Monsters that are displaced from suburban developments end up on display in schools, museums, or zoos. In Maricopa County, Arizona, local agencies handled 88 Gila Monsters between 1994 and 2002, many of which were processed through the Adobe Mountain Wildlife Rehabilitation Center near Phoenix (unpublished Arizona Game and Fish Department records 2003).

TABLE 22

Human–Gila Monster Encounters in Metropolitan Tucson

LOCATION	NUMBER
Yard	100
Garage	27
Porch/patio	17
By door	11
Swimming pool	7
Driveway	4
In house	4
In road	3
In bathroom	2
Playground	1
Dog's mouth	1
Under car	1
In kitchen	1
At school	1
In bedroom	1

NOTE: Reported to the Rural–Metro Fire Department in 2001.

ROAD KILLS

Roads have many negative impacts on wildlife, ranging from direct mortality from cars to habitat degradation (Trombulak and Frissell 2000). Apart from losses owing to large-scale habitat conversion, road kill is probably the largest source of human-caused mortality throughout most of the range of both Gila Monsters and Beaded Lizards. Although there are no estimates for the impact on helodermatid lizards, there is no question that large numbers are killed each year by automobiles on the increasing number of roads that accompany human expansion. Rosen and Lowe (1994) estimated that nearly 4,000 snakes were killed over 4 years on a 44-km stretch of a two-lane highway in southern Arizona. During one trip to Alamos, Sonora, in August 2002, we encountered 6 Beaded Lizards killed on a 10-km stretch of highway over 6 days (see plate 33). The slow, deliberate pace of helodermatid lizards makes them highly vulnerable to the automobile. Whereas some drivers brake or steer to avoid running over a *Heloderma* crossing the road, others have been observed to swerve to hit an ambling Beaded Lizard. Snakes that are dispersing, such as young of the year or males looking for mates, are more likely to be killed on roads, as are snakes that forage widely (Bonnet et al. 1999). Likewise, helodermatid

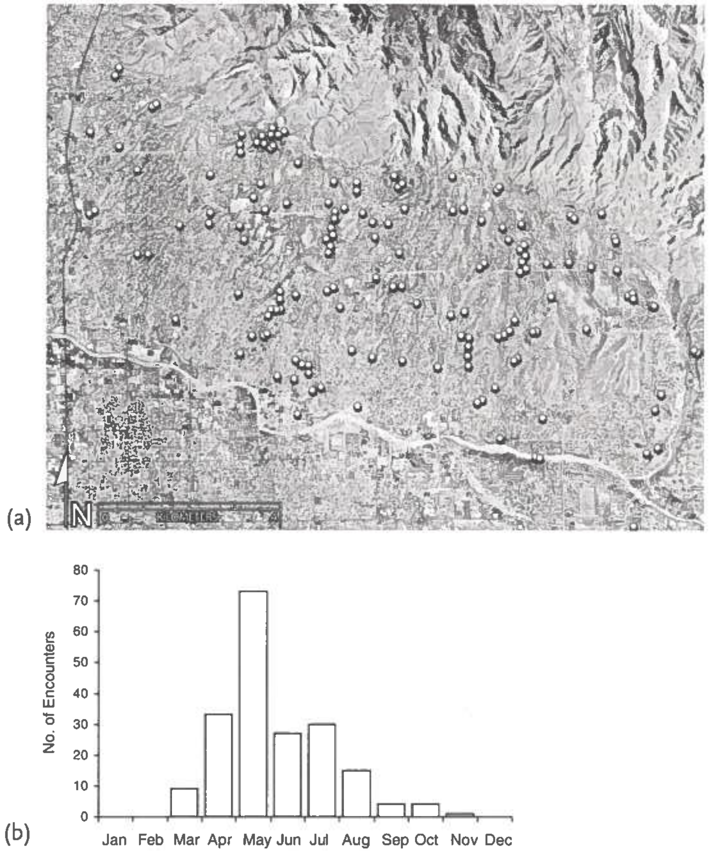


FIGURE 56. Spatial (a) and temporal (b) patterns of 196 Gila Monster encounters by residents near Tucson, Arizona, reported to the Rural–Metro Fire Department in 2001. In Tucson, May is known as "Gila Monster month" when many encounters occur (dots on aerial photo) in suburban areas of the Catalina Mountain foothills (see also table 22).

lizards are more likely to be struck by cars during periods when they show the greatest activity, such as May and August (chap. 5). Juvenile Gila Monsters are most frequently encountered on roads during the warm nights of May through August, when they are dispersing from nests. They may likewise be more vulnerable to mortality on roads during these periods.

PETS

Dogs and cats are a major source of mortality for many wildlife species (Patronek 1998; Koenig et al. 2002). Of 757 documented deaths of Blue-tongue Lizards (*Tiliqua scincoides;* a skinklike lizard about the size of a Gila Monster), in suburban Australia between July 1994 and March 1998, over half (394) were killed by domestic dogs and cats (Koenig et al. 2002). With the potential for a painful, venomous bite, an adult Gila Monster may be a formidable adversary for a dog or cat. Nevertheless, many domestic pets (usually dogs) are bitten by Gila Monsters each year, and some Gila Monsters are likely killed in these encounters. Of 21 Gila Monster bites reported to the Arizona Poison and Drug Information Center in Tucson during 2001 and 2002, 12 (57%) involved dogs. The fate of the Gila Monster is rarely reported in such cases; in two of the above cases (17%), it was noted that the dogs had killed the Gila Monster. Although most domestic cats likely avoid encounters with adult Gila Monsters, juveniles, which are often active at night, may be particularly vulnerable to predation by cats. In suburban Sydney, Australia, most of the Blue-tongue Lizards killed by cats were juveniles (Koenig et al. 2002).

COMMERCIAL TRADE

Commercial exploitation of helodermatid lizards began not long after Western culture became aware of their presence. By the 1880s a brisk commercial trade had developed (see Bogert and Martín del Campo 1956 and D. E. Brown

and Carmony 1991 for an interesting history of commercial trade in Gila Monsters). In 1887, Gila Monsters were being sold in Tucson for 50 cents to a dollar, and, by 1900, hundreds of the lizards had been captured and sold live for display in menageries and to institutions throughout the United States and Europe.

With the advent of the automobile came a second wave of commercial exploitation. In an effort to capitalize on the growing number of highway tourists, zoos and reptile gardens sprang up like spring wildflowers along roadways in the southwestern United States. In addition to live Gila Monsters, dead ones were sold as souvenirs mounted on cactus branches, or their skins as hatbands, billfolds, and belts. In 1930, live animals sold for between $2.50 and $7.00 and mounted specimens for $5.00 to $7.50 (Bogert and Martín del Campo 1956; D. E. Brown and Carmony 1991). No statistics were kept on commercial traffic in helodermatid lizards during this heyday of exploitation. Certainly thousands were removed from the wild and bought or sold during in the first half of the twentieth century. An article published in 1924 in the *Arizona Daily Republic* of Phoenix touting the economic benefits of the Gila Monster trade explained that a local dealer had "a selection of 200 of them for you all alive and happy and fat, and in any size you wish . . ." (Bogert and Martín del Campo 1956). In 1952, commercial traders were paying up to 50 cents an inch for Gila Monsters and selling them for up to $2.00 an inch (Mulch 1952). Such prices ($20 to $40 for an adult) were strong incentives for would-be Gila Monster dealers.

As commercial exploitation of Gila Monsters increased, so did concerns about their vulnerability to extinction. As early as 1890, Shufeldt wrote that "collectors are now rendering it scarce over nearly all of its range." By the 1930s, the scientific community began to argue that the Gila Monster should be protected from needless killing and overexploitation (Arrington 1930; Woodson 1943a). One outspoken advocate, Herbert Stahnke of Arizona State College, lectured widely on the topic in the 1940s and 1950s and successfully introduced legislation in Arizona promoting protection for the Gila Monster (D. E. Brown and Carmony 1991). In 1950, Arizona became the first state to outlaw killing or collecting *H. suspectum* without a valid permit (Grant 1952).

In other states (Utah, Nevada, and California), however, roadside zoos continued to sell Gila Monsters throughout the 1950s and 1960s. In St. George, Utah, where Gila Monsters were once abundant, a well-known auto salvage yard operator paid 50 cents a Gila Monster to children and local collectors who scoured the surrounding hills in search of the lizards. He then sold the Gila Monsters to supply houses and tourists. Andrew Barnum, a respected professor at Dixie College in St. George, estimated that hundreds of Gila Monsters had passed through this dealer in the late 1950s and early 1960s. Many of these lizards, as well as Desert Tortoises, were sold at roadside zoos and curio shops along old U.S. Highway 91, which passed through St. George, Utah, through the eastern Mohave Desert toward Las Vegas and Los Angeles.

By the 1970s other states finally followed Arizona's lead and passed laws that regulated the taking and sale of *H. suspectum* throughout its range, including Mexico. In addition, the Lacey Act amendments of 1981 prohibited keeping or transporting any wildlife, including Gila Monsters, that was obtained in violation of any state or tribal law or regulation (see Current Conservation and Legal Status, below). Therefore, keeping wild-caught Gila Monsters became illegal throughout the United States without a valid collecting permit from the state where the lizard originated. Today, most permits for wild-caught Gila Monsters are issued for lizards displaced by housing or recreational developments and turned in to wildlife officials. Such permits are normally given only to those engaged in legitimate scientific research or education.

Wildlife laws finally took much of the pressure off wild populations, and commercial exploitation of helodermatid lizards was curbed considerably. The secretive habits of helodermatid lizards, and their general rarity in nature, have also made it difficult for them to be exploited to the same extent as many other wildlife species. Today, relatively small numbers of Gila Monsters and Beaded Lizards are reported in legal international trade records. For example, 40 export permits were issued under CITES (see Conservation Status, below) by the U.S. Fish and Wildlife Service in 1994. Between 1998 and 2002, 45 permits were issued for *H. suspectum* and 12 for *H. horridum* (U.S. Dept. of Interior unpublished records; however, export permit numbers do not translate directly to the number of animals exported). International trade will likely increase as demand for keeping helodermatid lizards in captivity appears to be growing.

Domestic trade in captive-bred *Heloderma* is also on the rise. Although state laws within the United States generally prohibit keeping captive Gila Monsters in the states in which they naturally occur (Utah, Nevada, California, Arizona, New Mexico), captive-bred animals of both species can be legally bought and sold in many other states. With their beautifully textured skin, bright colors, and striking stature, helodermatid lizards are very popular reptiles sold among captive breeders. With the advent of recent successes in captive propagation (see chap. 8), legal commercial trade is increasing. And for the successful breeder this can be lucrative. During 2002, a conservative estimate of at least 200 Gila Monsters were hatched by captive breeders in the United States (M. Seward, pers. comm.) and these animals sold fairly easily to an eager market. As of 2004, Mexican Beaded Lizards *(H. h. exasperatum* and *H. h. horridum)* sell for $1,200 per lizard, as do Reticulate Gila Monsters *(H. s. suspectum)*. Banded Gila Monsters readily sell for $1,600 to $2,000 per lizard. In Japan, individuals have reportedly sold for $4,000. These prices reflect a very strong demand and a weak supply.

POACHING AND ILLEGAL TRADE

With helodermatid lizards commanding such lucrative prices in the captive-reptile market, the potential for illegal trade is enormous. Gila Monsters and Mexican Beaded Lizards are among the most common black-market reptiles in the southwestern United States (author's pers. comm. with Arizona Game and Fish Department and FWS law enforcement specialists). In the United States, the banded morph *(H. s. cinctum)* may be under particularly great pressure because of its rarity in the Mohave Desert and its value in the captive market. (Poaching is a significant threat to the diminishing populations in southwestern Utah, and enforcement activities have picked up there. In the late 1980s, a pet shop owner near Salt Lake City, Utah, was arrested after paying collectors to bring Gila Monsters from St. George to sell to pet shop customers).

Allowing trade in captive-bred *H. suspectum* provides a loophole for illicit collectors to launder lizards through the trade, or illegally capture wild *Heloderma* for breeding stock (*Federal Register*: August 28, 1996, Vol. 61, No. 168, p. 44324). Many recent arrests in Arizona provide examples. Reptile dealers from California and other states are occasionally (two to five per year) caught after poaching Gila Monsters in Arizona, then presenting false or erroneous permits for keeping wild animals in captivity (author's pers. comm. with Arizona Game and Fish Department law enforcement). California currently grants permits to private individuals to keep *H. s. suspectum*, but not *H. s. cinctum*, which occurs naturally in California.

There is also evidence of significant illegal trade in both species of *Heloderma* across the international border. Customs officials at border inspections frequently encounter Beaded Lizards and Gila Monsters. Poached lizards have been confiscated from autos of illicit collectors: from door panels, spare tire carriers, and trunks (among other places). Two recent cases involved smuggling both *H. horridum* and *H. suspectum* from Mexico in the floor panels of small aircraft. Customs agents discovered the illicit animals during routine inspections and the violators (in both cases, well-known reptile dealers) were prosecuted for felonies. Fines in such cases typically exceed $10,000, plus restitution expenses. Violators may be put on probation and lose their right to hold or apply for future wildlife permits. The Criminal Fines Improvement Act of 1987 increased the fines under the Lacey Act for felonies to $250,000 for individuals and $500,000 for organizations. Illicit trade across the U.S.–Mexico border appears to be variable. Some years there may be fewer than 20 cases, whereas in other years there may be considerably more. Immediately after September 11, 2001, when surveillance at the U.S.–Mexico border increased, the number of confiscations of Beaded Lizards and Gila Monsters transported across the international border also shot up. Dealers from Europe have also been arrested after poaching Gila Monsters in Arizona and attempting to transport them overseas (author's pers. comm. with FWS law enforcement).

One would hope that such unscrupulous elements are gradually being forced out of the reptile trade and that a majority of reptile dealers conduct their businesses ethically. Indeed, most dealers in the reptile trade who are successfully breeding helodermatid lizards are conservation minded and law abiding. Many strive to educate their peers and customers about wildlife laws and conservation issues, and many have a genuine desire to use captive animals for education and research. Captive breeders generously provided data and photographic documents for this book. Recent successes in captive breeding have helped shed light on reproductive cycles and incubation conditions for eggs, a discovery that could provide a better understanding of the reproductive biology of helodermatid lizards in nature (e.g., Applegate 1991; Strimple 1995; Seward 2000). Such information may aid conservation efforts that require an understanding of nesting biology. Herpetoculturalists can also help to internally police their peers and to help keep out unscrupulous elements. Many of the tips that have allowed law enforcement officers to catch *Heloderma* poachers have come from vigilant captive-reptile dealers.

It is difficult to know the real numbers of poached and smuggled lizards, but in some parts of the range of *Heloderma*, they could pose a significant threat, especially if left unchecked. Wildlife law enforcement has been relentless in tracking down and prosecuting violators. Enforcement officials use dogs, decoys, informants, and a variety of other methods to track, capture, and prosecute violators. Enforcement continues to improve as information is more easily shared and methods for detecting illicit trade become more sophisticated. Officials at the U.S. border with Mexico are becoming better educated about illicit trade in reptiles.

Nevertheless, poaching and illicit trade remain a threat to helodermatid lizards. As long as *Heloderma* remain among the most commercially valuable reptiles in North America, helodermatid populations throughout their range will continue to be exploited by illegal commercial and private collectors. As the supply of legal, captive-bred animals increases, the demand may go down. However, lower prices resulting from the greater supply may serve to increase the demand. A reliable supply of captive-bred animals could theoretically reduce the pressure on natural populations from threats of poaching. Because they interface directly with the consuming public, reptile dealers are important links in conservation of helodermatid lizards (see, for example, Seward 2000). Reptile dealers should work closely with conservation biologists to disseminate accurate information on natural history and conservation. Reptile dealers should strive to inform their customers about the vulnerability of certain reptile populations and the consequences of those who violate wildlife laws. The captive-reptile industry, the scientific community, and law enforcement must work together to prevent the commercial trade in captive helodermatid lizards from harming the integrity of populations in nature. Responsible captive breeders continue to be an important resource for enforcement officials by "internally policing" suspicious acquaintances. With cooperation, education, and careful monitoring to keep people honest, wildlife laws may prevent *legal* commercial trade from depleting natural populations, but illegal trade will likely remain a threat to which we must continually remain vigilant.

CURRENT CONSERVATION AND LEGAL STATUS

NATIONAL AND INTERNATIONAL STATUS

Both species of helodermatid lizards receive full legal protection from collecting, transport, and killing throughout their ranges. *Heloderma horridum* and *H. suspectum* have been listed since 1975 by the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) as Appendix II species. Appendix II includes species, such as wood bison and tegu lizards, in which trade must be controlled in order to avoid overexploitation. International trade in specimens of Appendix II species may be authorized by granting an export permit or reexport certificate; no import permit is necessary. A CITES permit is issued by the originating country only if the relevant authorities are satisfied that certain conditions are met, above all that trade will not be detrimental to the survival of the species in the wild. In the United States, the U.S. Fish and Wildlife Services issues permits only if documentation is provided that proves legal origin—including a complete paper trail back to legal founder animals. More rigid protection is provided for species listed under Appendix I of CITES. Appendix I includes species, from gorillas to Komodo Monitors, threatened with extinction. Trade in CITES Appendix I species is prohibited except under exceptional circumstances such as scientific research.

In 1996, the Humane Society of the United States, supported by several other environmental organizations, submitted a proposal to transfer *H. suspectum* and *H. horridum* from CITES Appendix II to Appendix I, stating that habitat loss and illegal trade put both species at sufficient risk to warrant stronger protection (Federal Register Notices 1996). They requested that the U.S. Fish and Wildlife Service take the case to the annual meeting of CITES members, the Council of Parties. The U.S. Fish and Wildlife Service solicited comments and new information, but in the end there were few comments and too little information to provide sufficient evidence that either *H. suspectum* or *H. horridum* met the criteria for inclusion in Appendix I (Federal Register Proposed Rules 1997). A second request to transfer *H. suspectum* and *H. horridum* to Appendix I, submitted by the Humane Society and the International Wildlife Coalition in 1999, was again declined based on similar grounds (Federal Register Notices 1999). Both *H. horridum* and *H. suspectum* remain CITES Appendix II species.

Both species of helodermatid lizards are included on the World Conservation Union (IUCN) "Red List." Species throughout the world are evaluated by the IUCN and ranked within categories, based on a combination of population characteristics and geographic distribution, which are widely used for identifying taxa that may be at risk of extinction. *Heloderma suspectum* and *H. horridum* appear on the Red List under the "Threatened" category as "Vulnerable" species (IUCN 1994). A taxon is deemed "Vulnerable" when it is not "Endangered" but is facing a "high risk of extinction in the wild in the medium-term future" as defined by population trends and geographic distribution (IUCN 2001).

In Mexico, helodermatid lizards are listed as "Threatened" (in Spanish, "Amenazadas") under the Mexican equivalent of the U.S. Endangered Species Act (NORMA 2001). The threatened category from Mexican law coincides, in part, with the "Vulnerable" category of the IUCN Red List. It defines *threatened* as species or populations that could become at risk of extinction in a short to medium period if negative factors (such as those described above) continue to operate that reduce population sizes or alter habitats.

In Guatemala, *H. horridum charlesbogerti* is listed on the Guatemalan "Lista Roja" (Red List) as "threatened," a category that, in principle, is equivalent to its Mexican counterpart.

In the United States, the Gila Monster was listed under the U.S. Endangered Species Act in the 1970s as a "Threatened Species," but it was removed from the list as additional information suggested that populations within the core of their geographic distribution were not at risk. Today, *H. suspectum* is listed under the Endangered Species Act as a "Species of Concern" and within Federal Category 3/3C Candidate. This means that they were once considered for listing, though not any longer; 3C means that *H. suspectum* was found to be more common than once thought. However, the spotty distribution of the Gila Monster in the Mohave desert of the American Southwest, and rapid urban and recreational development in that region, prompted the U.S. Fish and Wildlife Service in 2001 to list the Gila Monster as a high-priority species that may be vulnerable for listing as a threatened or endangered species in the foreseeable future.

An additional ranking system has been developed by the Nature Conservancy and the Natural Heritage Network to identify species and ecosystems at risk. Each species is assigned one global rank (called a G-rank), which applies across its entire range; a national rank (N-rank) for each nation in its range; and a subnational rank (S-rank) for each state in its range. Subspecies are assigned "infraspecific taxon" ranks (or T-ranks). Ranks are based on a sliding scale of 1 to 5, 1 being "critically imperiled" and 5 being "demonstrably widespread, abundant and secure." This ranking system (Heritage Status Rank), assigns a rank of G4, N4, T4 to both *H. suspectum suspectum* and *H. s. cinctum* (*H. horridum* has not yet been ranked by this system). A rank of 4 means "Apparently Secure." The S-ranks for *H. suspectum* (summarized below) vary from state to state, reflecting vulnerability of populations along the margins of their range (NatureServe Explorer 2002).

Helodermatid lizards are also protected under provisions of the U.S. Lacey Act, which controls commerce in illegally taken fish and wildlife. Under the Lacey Act, it is a federal crime to "import, export, transport, sell, receive, acquire, or purchase" any wildlife, alive or dead, that was obtained in violation of any state or tribal law or regulation. In the United States, *H. suspectum* receives legal protection in every state in which it occurs. State laws prohibit collecting or killing Gila Monsters without special permits, usually given only for legitimate scientific or educational purposes. The Lacey Act, therefore, provides an additional level of legal protection. The conservation and legal status of the Gila Monster in each state in which it occurs in the United States is summarized in the following sections.

ARIZONA

In the first legal protection offered to any venomous animal, the state of Arizona outlawed killing or collecting Gila Monsters in 1952 (Grant 1952). The Arizona office of the U.S. Bureau of Land Management (BLM; the federal agency responsible for managing the majority of public lands harboring Gila Monster habitat) lists *H. s. cinctum* populations north and west of the Colorado River (known as the "Arizona Strip") as a "Species of Concern" and the Banded Gila Monster appears on their "Sensitive Species List" in 2000. Criteria for BLM Sensitive Species (Manual Section 6840) include "those that are under status review by the Fish and Wildlife Service or whose numbers are declining so rapidly that Federal listing may become necessary; or with typically small and widely dispersed populations; or those inhabiting ecological refugia or other specialized or unique habitats." The Heritage Status Rank in Arizona for both *H. s. suspectum* and *H. s. cinctum* is S4 (Apparently Secure).

CALIFORNIA

In California the Gila Monster is listed as a "Species of Special Concern" (California Department of Fish and Game 1994). *Heloderma suspectum cinctum* is listed in the California Department of Fish and Game's Natural Diversity Database as extremely endangered owing to its rarity in the state (see chap. 2). The Heritage

Status Rank for *H. s. cinctum* in California is S1/S2 (Extremely Imperiled/Imperiled).

NEW MEXICO

Although Gila Monster populations appear stable in New Mexico (Degenhardt et al. 1996), *H. s. suspectum* is listed as endangered because of its extremely limited distribution in that state. The Heritage Status Rank for *H. s. suspectum* in New Mexico is S1/S2 (Extremely Imperiled/Imperiled).

NEVADA

Gila Monsters are listed in Nevada as "fully protected" and a "High Priority Evaluation Species." *Heloderma suspectum cinctum* in Nevada has been assigned a Heritage Status Rank of S2 (Imperiled).

UTAH

Heloderma suspectum cinctum is listed in Utah as one of only two State Endangered Species of reptiles, the other being the Desert Tortoise (*Gopherus agassizii;* Fridell et al. 1998). Utah defines State Endangered Species as "any wildlife species or subspecies which is threatened with extirpation from Utah or extinction resulting from very low or declining numbers, alteration and/or reduction of habitat, detrimental environmental changes, or any combination of the above. Continued long-term survival is unlikely without implementation of special measures. A management program is needed for these species if a Recovery Plan has not been developed" (State of Utah, Division of Wildlife Resources Policy Number W2AQ-4 [1998]: State Sensitive Species). Although no management program had yet been formalized for the Gila Monster in Utah, a management strategy has been initiated by the Utah Division of Wildlife Resources (McLuckie et al. 2004). Huge efforts to protect Desert Tortoise habitat in Utah, much of which is shared with *H. s. cinctum*, may benefit Gila Monsters (see below). In addition, Utah law prohibits disturbing a den of any reptile or killing, capturing, or harassing any reptile within 100 yards of a reptile den without first obtaining a certificate of registration from the Utah Division of Wildlife Resources. The Heritage Status Rank for *H. s. cinctum* in Utah is S1 (Critically Imperiled).

VULNERABILITY

Helodermatid lizards receive a good measure of legal protection throughout their range. Apparently many robust *Heloderma* populations still exist in the wild, although we know relatively little about the size of such populations or where they occur (chap. 6).

Just how vulnerable are the helodermatid lizards? A species' vulnerability to extinction is affected by its geographic range, population size, and habitat specificity (Rabinowitz et al. 1986; Myers 1997). Each species of *Heloderma* shows a fairly broad geographic distribution. This could change, however, if *H. horridum alvarezi* and *H. h. charlesbogerti* (which show restricted geographic ranges) are combined into a separate species, as genetic evidence suggests they might be (Douglas et al. 2003; chap. 2). Throughout their range, helodermatid lizards are not habitat generalists but instead tend to select specific habitat types (chap. 5). Although population densities may vary among habitats and over time, helodermatid lizards rarely show high population densities anywhere throughout their range (chap. 6). These traits certainly suggest that helodermatid lizards are vulnerable, an attribute recognized by wildlife regulators in designating legal protection for helodermatid lizards as discussed above. *Heloderma* populations may be in the most trouble along the margins of their geographic range. The biggest threats are in the Mohave Desert at their northern terminus and in southern Mexico and Guatemala at the southern edge.

CONSERVATION OPTIONS AND STRATEGIES

THE TORTOISE AND THE GILA MONSTER: A CASE STUDY

A useful context in which to envision conservation strategies for *Heloderma* may be provided by the Desert Tortoise *(G. agassizii)*, a well-known cohabitant with the Gila Monster throughout much of its range. Because of its widespread distribution, public support, and charisma, the Desert Tortoise has been called a "flagship" species—that is, one whose notoriety can help awaken public awareness that can leverage protection for other species as well (such as *H. suspectum* populations in the Mohave Desert).

In the early 1970s, biologists realized that populations of the Desert Tortoise were declining. In 1980, the Beaver Dam Slope population in southwestern Utah was federally listed as "Threatened" under the Endangered Species Act. Beginning in 1984, several conservation organizations proposed that the U.S. Fish and Wildlife Service list remaining Desert Tortoise populations. In 1990, after a serious upper respiratory tract disease had severely reduced several additional populations, and environmental organizations served notice of pending court action, the U.S. Fish and Wildlife Service listed the Desert Tortoise as "Threatened" across 30% of its range, specifically within the Mohave Desert of southwestern Utah, Nevada, and California, the "Arizona Strip" region of northwestern Arizona, and portions of the lower Colorado River valley subdivision of the Sonoran Desert in California (K. H. Berry 1997). In consultation with a team of renowned scientists, the U.S. Fish and Wildlife Service developed a Recovery Plan for the Desert Tortoise that took 4 years to prepare.

The federal listing of the Desert Tortoise in the Mohave Desert and lower Colorado River valley closely coincided with a development boom and, as with the listing of spotted owls in the Pacific Northwest, put conservationists and developers on a collision course. Communities such as St. George, Utah, came under great pressure to accommodate the demand for real estate development while also protecting a federally threatened species in its backyard. To allow for some tortoise losses that were incidental to (but not the primary purpose of) land development (termed *incidental take* under the Endangered Species Act), extensive habitat conservation plans (or HCPs) were developed for Washington County, Utah, and Clark County, Nevada. In Washington County, Utah, a permit was issued that allowed 12,264 acres of habitat and 1,169 tortoises to be "taken" for development, while a 61,000 acre reserve (the Red Cliffs Desert Reserve) was established that contained just over 38,000 acres of suitable habitat for Desert Tortoises.

The Washington County Habitat Conservation Plan sought to reconcile the economic benefits of the real estate boom with accelerating habitat losses in southwestern Utah. This was no simple task, to say the least. Initiated in 1991, it took over 5 years and many millions of dollars to develop. The federal government will spend over $100 million to acquire private lands within the reserve, and Washington County has budgeted $9 million over 20 years for the tortoise take permit (Bill Mader, pers. comm.). One of the challenges in Utah (where some of the best-known populations of Gila Monsters in the Mohave Desert were also known to occur) is that tortoises occupy habitats restricted to below 3,500 ft in elevation, the very locations which make attractive places for recreational developments and retirement communities (Crowther 1993). This makes acquisition of sensitive tortoise habitat difficult and very expensive.

In the 14-plus years (from 1980 to 1994) between agency acknowledgment that the tortoise was in trouble and establishment of a Recovery Plan for the Mohave Desert and lower Colorado River valley Desert Tortoise populations, the human population of the region more than tripled, as did the attendant pressures on desert wildlife. The costs of habitat acquisition (where habitat was still available to be acquired) shot up in proportion to the increasing human population. Millions of dollars have been spent on trying to recover declining populations of Desert Tortoises, yet throughout most of their range in the Mohave Desert, tortoise populations continue to decline (K. H. Berry 2003).

At the same time that the Desert Tortoise was listed as an endangered species, the scientific community recommended ways that the goals of the Endangered Species Act might be better achieved by strengthening the use of science (Carroll et al. 1996). The scientists' recommendations echo the lessons learned from the Desert Tortoise listing: species are less likely to be threatened with extinction and can be protected at a lower cost if a more proactive approach is used to protect biodiversity. The time to consider recovery and management of a species is before it approaches the endangered species list. Management options, and chances for success, are usually greater before the geographic range of a species, and its total population size become seriously reduced (Carroll et al. 1996).

The Ecological Society of America recommended that science could be applied more effectively under the Endangered Species Act by protecting habitats, not just species. One way to do this is to use currently endangered species as "umbrella species" that afford protection to other species that share the same habitat (Carroll et al. 1996).

Much research continues on Desert Tortoise recovery, and lands continue to be set aside and managed to protect Desert Tortoise habitat. As efforts to restore Desert Tortoise populations continue, the role of *G. agassizii* as an umbrella species for *H. suspectum,* and other species, should be kept in clear focus by conservation biologists and land use planners. The geographic ranges of *H. suspectum* and *G. agassizii* overlap considerably. Gila Monsters are often found in high-quality tortoise habitat; indeed, some Gila Monster populations may even depend to some extent on tortoise eggs as a food source.

As no two species have exactly the same ecological requirements, the umbrella species concept has its limitations, and *G. agassizii* may not be the perfect umbrella for *H. suspectum.* The position of *Heloderma* as a nest predator places it at a trophic level that precludes an ability to maintain population densities as high as the herbivorous Desert Tortoise. For example, in the 1980s, Paradise Canyon, Utah, supported approximately 20 to 25 Gila Monsters per square mile (Beck 1985a), one of the highest documented population densities of Gila Monsters known at the time (see chap. 6). During the same period, the tortoise population of Paradise Canyon numbered at least 150 individuals within the same square mile (Beck and Coombs 1984).

Nonetheless, the Desert Tortoise may be an important tool in preventing *H. suspectum* from reaching the threatened species list, given the limited options for habitat protection and the relentless pressures of human expansion in the Mohave Desert. In response to the Desert Tortoise listing, Clark County, Nevada, drafted a "Multi-species" Habitat Conservation Plan intended to protect the Desert Tortoise and other special status species in the Mohave Desert at risk from rapid development, off-highway vehicle use, and other urban-related threats (Clark County and U.S. Fish and Wildlife Service, 2000). In Utah, $2 million of the $9 million budget for Washington County's take permit has been allotted by the U.S. Fish and Wildlife Service to be spent on "other species" (Bill Mader, pers. comm.). Surveys for tortoises should also include surveys for Gila Monsters. Research funds spent on tortoises might also be wisely applied to understanding the resource needs of *H. suspectum.* Monies used to buy tortoise habitat might also include prime *Heloderma* habitat as well. In this way, perhaps repetition of the difficult and expensive history of protecting the Desert Tortoise may be avoided while also benefiting habitat for Gila Monsters.

CONSERVATION STRATEGIES

The best hope for protecting remaining populations of helodermatid lizards is to employ a proactive conservation strategy. Such a strategy would involve identifying populations or habitats at risk and taking steps to manage and protect habitats necessary for maintaining viable populations. This would require a more complete understanding of resource demands and critical habitat features, of the location of populations (and their densities) and of genetic diversity among populations of helodermatid lizards.

HABITAT PROTECTION AND RESTORATION

The best way to protect populations is to protect their habitats. If ample habitats could simply be left alone, helodermatid lizards might do just fine on their own without any "management" whatsoever (as long as they are protected from harvesting). Options for setting aside pristine habitat are becoming increasingly rare as more humans settle in the southwestern United States, and *Heloderma* habitats continue to become more degraded and fragmented. Habitat protection may include a range of options, from complete exclusion of people to carefully controlled management, but a basic goal of any habitat protection would be a clear long-term management strategy for maintaining viable populations.

There are many areas within the range of *Heloderma* that are being managed (or could be managed) based on this goal. In the United States, lands in national parks and monuments, BLM wilderness areas, state parks, Indian reservations, military reserves, and county parks (among others) provide varying degrees of protection for Gila Monsters. The Red Cliffs Desert Reserve near St. George, Utah, set aside for the endangered Desert Tortoise, also serves to protect other species, including *H. suspectum.* In a short section considering impacts to Gila Monsters, the Washington County Habitat Conservation Plan for the Desert Tortoise stated that "elimination of several population pockets of this unique lizard is expected to occur as a result of the HCP implementation. However, the species is expected to benefit from reserve establishment in areas such as Paradise Canyon." (Washington County Commission 1995). Our best hope of protecting remaining populations of Gila Monsters in Utah may, in fact, be the Red Cliffs Desert Reserve.

In Mexico, several national parks and biosphere reserves provide limited protection to *Heloderma.* One of the best known is the Chamela-Cuixmala Biosphere Reserve in coastal Jalisco, which includes the biological field station at Chamela where I conducted field research on *H. horridum.* The reserve affords protection to about 13,000 hectares (52 square miles) of high-quality tropical dry forest habitat for *H. horridum* and many other species. The future of the region is uncertain, however, as increasing pressure for development of coastal tourist resorts and clearing of forest for agriculture pose perennial challenges to the maintenance of its long-term biological integrity. Other areas in Mexico affording protection to tropical dry forest habitats of *H. horridum* include El Ocote Ecological Reserve along the border of Oaxaca and Chiapas, which serves as a biological corridor for numerous species. CONABIO (Comisión Nacional para el Conocimiento y Uso de la Biodiversidad) has identified several other regions in Mexico that warrant protection and efforts are under way to prevent these habitats from being destroyed (García-Aguayo 2003). Because many of the locality records for both species of *Heloderma* fall outside the boundaries of these proposed protected areas (fig. 55), well-informed input to reserve planners about the distribution of *Heloderma* populations becomes especially important.

Efforts are also under way by the Guatemalan government to set aside a reserve for the Guatemalan Beaded Lizard, *H. h. charlesbogerti.* The regional park, *El Niño Dormido* ("the sleeping baby") would protect a portion of tropical dry forest habitat for this rarest subspecies of *H. horridum* in the Motagua Valley of eastern Guatemala.

MANAGING RESERVES Many of the principles that govern good conservation management apply to managing desert and tropical dry forest habitats of helodermatid lizards, namely (1) ecological processes and biodiversity must be maintained, (2) external threats must be minimized, (3) evolutionary processes must be conserved, and (4) management must be adaptive and minimally intrusive (see Carroll and Meffe 1997). How can these principles be applied to habitat reserves? First, a reserve must be large enough to sustain a viable population, not just individuals. Important corridors that link quality habitat areas within the reserve boundaries should be identified and protected (see below).

Second, managers must identify key habitat features, such as shelters, plant communities, prey populations, and potential nest sites. Prey populations (e.g., cottontail rabbits in Utah) and microhabitats that are especially sensitive, such as shelters or nest sites, should be monitored. Because managers need species-specific information on habitat use, diet, activity patterns, and population trends, monitoring and research programs should be established within and around a reserve that generate information about the status of its inhabitants and serve to guide management strategies.

Third, key habitat features must be protected and human use of the reserve (recreational and otherwise) must be managed so that these resources are not compromised. Negative impacts of human activities must be minimized, especially within the core of a reserve and around sensitive areas. In some cases, access should be restricted. For some reptiles, even what seem to be innocuous recreational activities such as fishing and hiking may be linked to population decline. In wood turtles, recreation activities resulted in a significant population decline (as a result of reduced recruitment and loss of adult females), even though habitat quality appeared to remain unchanged (Garber and Burger 1995). Dogs, cats, and off-road vehicles should be prohibited from any sensitive region and from core areas of a reserve.

Finally, users must be educated about protecting *Heloderma* and their habitat. A reserve is doomed to fail if humans who use it do not see the value of protecting biodiversity. A successful reserve would include an active program in public education. Managers would encourage citizens to play an active role in helping to protect the biological integrity of a reserve (plate 35).

BUFFER ZONES When management areas are small with respect to the resource needs of the species they contain (which is likely the case for the Red Cliffs Desert Reserve), semiwild lands around a protected area (buffer zones) can serve to increase its effective size (Carroll and Meffe 1997). The margins of a reserve, therefore, can be extremely important for helping to maintain the biological integrity of its core. One way to do this is to manage growth along margins of habitat reserves to provide a buffer. Housing density should be kept lower, native vegetation and habitat heterogeneity (e.g., boulders and burrows) should be retained, and habitat corridors should be maintained/established wherever possible (below). As housing density increases, pavement replaces natural vegetation and habitat becomes fragmented and diminished (Germaine and Wakeling 2001). Domestic pets, such as cats and dogs, must be prevented from harming wildlife along the margins of a reserve. If they take pride in living next to a reserve, human residents along a buffer zone can play a crucial role in its management by participating in surveillance and protection.

Habitat protection, therefore, is not, and should not be, the sole responsibility of public agencies. Private landowners may be some of the best habitat stewards. Through education, working with public officials to monitor habitat conditions, and remaining vigilant to poaching and other illegal activities that harm habitats, private landowners can be a crucial link in ensuring the long-term viability of *Heloderma* populations. Information for homeowners about Gila Monsters is available from the Tucson Herpetological Society, and the Washington County, Utah, Red Cliffs Desert Reserve in St. George. Landowners may formalize protection through conservation easements or agreements, which are facilitated by public or private agencies, such as the Nature Conservancy.

CORRIDORS Where habitat reserves are fragmented, as is often the case, habitat corridors become particularly important. Corridors that provide a habitat bridge for movement of individuals between habitat patches must be maintained, or established, wherever possible. For example, a population viability analysis of the Acorn Woodpecker, which lives in small, isolated populations in the southwestern United States and Mexico, showed that most populations would become extinct within 20 years if they became completely isolated. With only a small amount of migration among populations, however, most of the populations were predicted to persist for over 1,000 years (Stacey and Taper 1992). Although birds are obviously more mobile than Gila Monsters, the study illustrates an important principle in conservation biology: population viability is greatly enhanced, and extinction risk reduced, when corridors allow movement of individuals, and gene flow, among isolated populations (Carroll et al. 1996). Paradise Canyon provides such a corridor between two major sections of the Red Cliffs Desert Reserve near St. George, Utah.

RESTORATION Habitats of helodermatid lizards have been degraded in many ways: by agriculture, grazing, invasion of exotic species, off-road vehicle use, and other forms of uncontrolled recreation. As a growing proportion of natural habitats becomes degraded by human activities, restoration of those habitats will become necessary. Because the process of succession occurs very slowly in deserts, restoration of disturbed desert habitats takes much time (MacMahon 1997). Some attempts to restore tropical dry forest habitats have met with at least marginal success (Janzen 1988b). Measures that can be taken to restore degraded habitats include programs to eradicate exotic grasses and control fire (Brooks and Pyke 2001). Residents living along the edges of *Heloderma* habitat can be encouraged to landscape with native plants that provide habitat for desert wildlife. Although habitat restoration can be an important conservation strategy in severely degraded habitats, it is expensive, difficult, and time consuming. For most *Heloderma* populations, it has yet to be tested.

In addition to repairing degraded habitat, a comprehensive restoration project for *Heloderma* might entail reintroducing individuals into previously occupied habitats (termed *repatriation;* Dodd and Seigel 1991) or releasing individuals into areas not known to contain the species (termed *translocation;* Dodd and Seigel 1991). Such practices have occasionally been performed unofficially in an effort to move individuals out of harm's way. At present, they are not considered effective strategies and should not be attempted without a more complete understanding of habitat requirements, structure, and dynamics of affected populations.

DISPLACED *HELODERMA* AND RELOCATION

Hundreds of helodermatid lizards are displaced each year by agricultural, residential, recreational, and commercial development. Some of these lizards are removed from urban or suburban areas and temporarily housed in facilities such as Arizona's Adobe Mountain Wildlife Rehabilitation Center. Many of these animals are well cared for and used for display and education in zoos and museums throughout the world. However, activities focused at caring for Gila Monsters displaced by humans should not be viewed as a substitute for reducing habitat loss and fragmentation. Even if well cared for in captivity, animals displaced by habitat loss are ecologically dead, at least in the wild.

Another option commonly used in managing "nuisance" wildlife (e.g., unwanted creatures that occupy people's homes, yards, or neighborhoods) is to move such "intruders" to areas that are not permanently inhabited by humans. Moving individuals out of harm's way, preferably to suitable habitat, is termed *relocation* (Dodd and Seigel 1991). Hundreds of venomous reptiles are relocated each year from metropolitan areas in the southwestern United States to nearby desert habitats (Hare and McNally 1997; Nowak et al. 2002; Sullivan et al. 2004). People generally feel better if they can release reptiles elsewhere rather than simply kill them. The assumptions behind such a practice are that (1) there is available habitat that may support the "intruder," (2) intruding wildlife would be better off if moved away from human habitation, and (3) human inhabitants will feel safer and more secure without the presence of "nuisance" species. Relocation of "nuisance" helodermatid lizards, therefore, brings three questions to mind: How effectively does moving a reptile away from a residence prevent the animal from returning? What are the prospects for survival of such displaced wildlife? And are humans and *Heloderma* really incompatible?

In a study conducted in metropolitan Phoenix, Arizona, Sullivan et al. (2004) monitored the fate of 25 "nuisance" Gila Monsters. These lizards were relocated from zero to 25,000 m from their point of capture. Of 18 Gila Monsters relocated less than 1,000 m, all returned to within a short distance of the site of capture within 30 days. This is not surprising given the strong fidelity Gila Monsters show to particular shelter sites (Beck and Jennings 2003; chap. 5). Short distance relocations, therefore, are not an effective means of removing Gila Monsters from the yards of homeowners because the lizards simply return to familiar territory. Of seven Gila Monsters relocated over one kilometer, however, none returned to the original capture area. Disturbingly, all of the relocated lizards either died or were lost, suggesting that relocated individuals did not readily tolerate their new environments (Sullivan et al. 2004). In addition, relocated Gila Monsters traveled nearly five times as far as nonrelocated individuals, most likely in an attempt to locate familiar territory. Relocated rattlesnakes have also been shown to travel farther than resident snakes and to suffer higher rates of mortality (Reinert and Rupert 1999; Nowak et al. 2002).

Relocation or translocation has proven useful for some species, such as Desert Tortoises, that have experienced significant population losses but for which suitable habitat still remains. In some areas, Desert Tortoises have been translocated with success (Nussear et al. 2000). Relocation is most likely to be successful when we have sufficient knowledge about population characteristics and habitat quality within an area to which individuals are to be moved (Dodd and Seigel 1991; Nussear et al. 2000). However, if a site is already at its carrying capacity, adding additional individuals will likely disrupt the current population structure and, at best, result in no net gain.

Helodermatid lizards show a structured social system (chap. 8), great fidelity to established territories (chap. 5), and population densities generally far below those of the Desert Tortoise (chap. 6). Moving lizards to new habitats outside of their familiar territory is a risky conservation strategy unless we have detailed knowledge about the ability both of the release site to absorb new individuals and of the displaced individuals to adapt to the release site. Unless there is some reason to expect that a particular habitat has "extra space" for additional Gila Monsters, relocation should not be considered an effective management strategy.

CAPTIVE PROPAGATION AND REPATRIATION

Reptile breeders have made progress in recent years in successfully inducing helodermatid lizards to reproduce in captivity (chap. 8). Some of what these breeders have discovered can be valuable for understanding the reproductive cycles and nesting biology of helodermatid lizards in nature and for education. Care must be taken, however, in jumping to the conclusion that captive reproduction can serve as a valid conservation strategy for repatriating helodermatid lizards in the wild. The prospect of captive propagation and repatriation should never draw attention away from the need to protect or restore natural habitats and cannot substitute for a failure to do so. If viable habitat does not exist, captive breeding can do little to bring a species from the brink of extinction in the wild. Moreover, individuals released in areas other than where their recent genetic stock originated may not be adapted to those environments (Carroll et al. 1996). In addition, deleterious alleles may increase in captivity and diseases may also be carried by reintroduced individuals. Captive propagation and repatriation as a conservation strategy for helodermatid lizards is a long way off. Such a strategy should be used only as a last resort. Let us hope that a time never comes when we are forced to rely on captive propagation programs to repatriate helodermatid lizards in the wild.

LIVING WITH *HELODERMA* IN OUR MIDST

Many of the hundreds of Gila Monsters that have been relocated over the years may not have survived long enough to reproduce in their new habitats, as shown by Sullivan et al. (2004). However, interesting results of the study by Sullivan et al. (2004) include both the degree to which human residents tolerated—and even appreciated—the presence of Gila Monsters and the degree to which Gila Monsters appeared to maintain high survivorship in habitat also occupied by people. According to Sullivan et al. (2004), "Numerous Gila Monsters that we moved less than 1,000 m were encountered (and tolerated) by homeowners, and regularly used refuges near original capture sites following relocation."

This suggests the possibility that under certain conditions people and *Heloderma* might peacefully coexist. Humans can easily understand the risks and benefits of living with wildlife. Just as responsible parents do not allow children to play with knives, children can be taught not to pick up a Gila Monster if they see one. (My kids understood this very well by the time they were two and a half years old.) And no one would allow a child too young to understand this to play alone outside unattended. Just as we accept many risks in our daily lives, such as stairways, electrical outlets, and automobiles, so too can residents, armed with an understanding of the minute risks of a Gila Monster in their midst, actually appreciate living with such a unique neighbor.

Given that helodermatid lizards have inhabited the southwestern United States and western Mexico for many thousands of years (and the genus *Heloderma* has survived for at least 23 million years), it is worthwhile considering who is the real intruder. With some vigilance, most people living in *Heloderma* habitats can learn to tolerate—and even appreciate—such a unique feature of the desert. So if you find a Gila Monster in your yard or neighborhood, be glad. You are fortunate. Its presence affirms that you live in an incredible place. Leave it alone and watch it go by. Moving Gila Monsters should never be used as a substitute for protecting their habitats, even if that habitat is also shared with humans. Suggestions for living with Gila Monsters are available from the Tucson Herpetological Society, the Arizona Game and Fish Department, the Utah Division of Wildlife Resources, and the Washington County, Utah, Red Cliffs Desert Reserve.

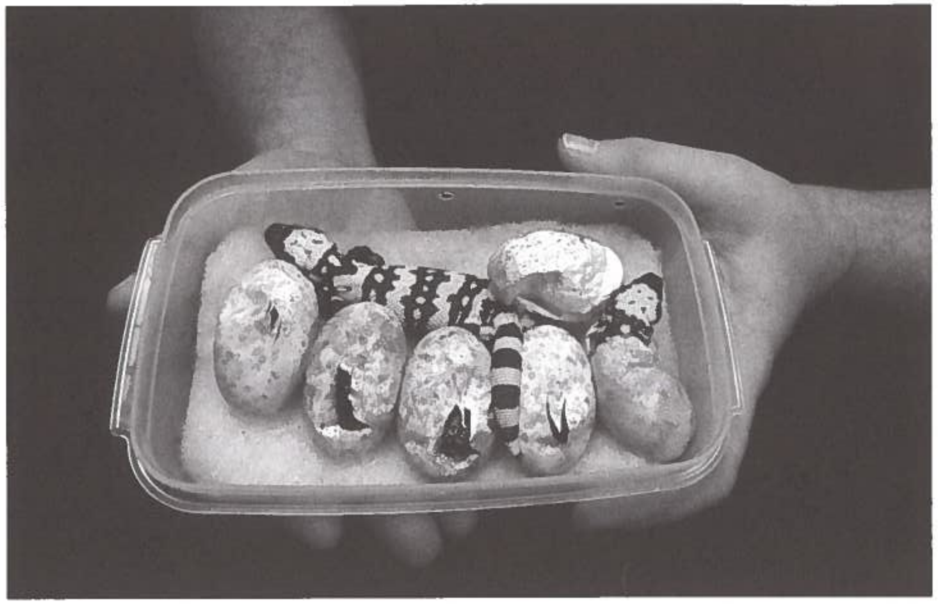


FIGURE 54. Mark Seward clutches a batch of captive-bred hatching Gila Monsters. Hatchlings use an egg tooth, or their sharp claws, to slice the leathery shell. They may remain within the opened egg for several days as they absorb precious yolk before emerging fully capable of defending themselves with a venomous bite.

Nevertheless, legally obtained helodermatid lizards are commonly kept in captivity, often as part of educational displays in zoos, museums, and schools. Hundreds exist in captivity in public and private collections around the world. Careful maintenance of legally captive animals provides opportunities for exposure to the beauty and wonder of these fascinating lizards and holds promise for developing greater appreciation, respect, and understanding. It is often at a zoo, school, or museum where the seed of appreciation is first planted in children (plate 35).

PARASITES AND DISEASES

Little is known about parasites and disease in wild helodermatid lizards. In captivity, they appear surprisingly resistant to sickness and disease. Urate deposits, which can lead to gout, have been reported in the pericardium of the Gila Monster (Appleby and Siller 1960). A number of internal helminth parasites (Goldberg and Bursey 1990, 1991; Upton et al. 1993) as well as ectoparasites (A. J. Smith 1910) have been identified from *H. suspectum*. In an analysis of 110 gastrointestinal tracts, Goldberg and Bursey (1991) discovered that Gila Monsters may be hosts to 1 cestode species *(Oochoristica whitentoni)*, two nematode species *(Oswaldocruzia pipiens*, and *Skrjabinoptera phrynosoma)*. These findings represent new host records. Helminth prevalence and mean intensity were 12% and 9.9%, respectively (Goldberg and Bursey 1991). Captive Gila Monsters show much higher loads of helminth parasites than do wild *H. suspectum* (J. Jarchow, pers. comm.).

CAPTIVE PROPAGATION

Much has been published about captive maintenance and reproduction of helodermatid lizards (e.g., Durham 1951; Benes 1968; Seward 2000; see references above). An important part of our knowledge of the reproductive biology of helodermatid lizards has been contributed by herpetoculturalists working in zoos and private collections who have successfully bred *Heloderma* in captivity (fig. 54). Because of impressive advances in captive propagation, helodermatid lizards are likely to become increasingly common in the pet trade. As I discuss in the chapter that follows, these beautiful animals bring lucrative prices in the captive pet market. Thus a strong incentive exists for the would-be captive breeder of helodermatid lizards. Captive breeding is far preferable to collecting animals from the wild, and responsible breeding programs could provide captive-bred animals that, in theory, help to alleviate pressure on native populations from illegal collecting.

The downside, however, is that captive trade in helodermatid lizards also provides an avenue for illicit trade. It can be difficult to know whether animals used for breeding purposes are captive bred or illegally poached (chap. 9). Anyone considering buying or breeding helodermatid lizards should consider the following: (1) It is not a good idea to keep venomous animals in captivity as pets. (2) Owners of illegally obtained, transported, or housed animals will be prosecuted! Fines for felonies under the Lacey Act can be $250,000 for individuals and $500,000 for organizations. (3) Keeping helodermatid lizards (indeed, any wildlife) in captivity entails a responsibility to promote conservation and education, to remain vigilant of illegally obtained animals, and to report suspicious individuals to wildlife authorities. (4) Captive animals can introduce disease and deleterious alleles into natural populations and should never be released into the wild. (5) Finally, poaching animals from the wild for use as breeding stock, or for sale, is dishonest, illegal, and harmful to native populations. Wildlife laws and enforcement are in place so that anyone caught participating in this abominable practice will be severely punished. If you think someone is illegally harboring a Gila Monster or Beaded Lizard, you are encouraged to contact local wildlife authorities! The risks of poaching continue to rise as wildlife laws become more aggressively enforced and wildlife agents become better informed and more vigilant. Commercial exploitation is not the only threat facing helodermatid lizards, however. In the following chapter, I'll discuss many others.

CHAPTER 10

Future Directions

. . . these are some amazing animals, and the more we learn about their physiology and ecology, the more exciting they get.

DALE DENARDO, 2003

JUST AS IT IS A GOOD TIME to protect habitats (while they still exist), it is now an excellent time to investigate the biology of *Heloderma*. People have long been interested in helodermatid lizards, but with recent technological advances in radiotelemetry, miniaturized dataloggers, and molecular biology there are unprecedented opportunities to answer a number of questions regarding their conservation biology, evolution, physiology, and ecology. With the discovery of biologically active peptides in the venom of helodermatid lizards (and the important pharmacological applications of those compounds, such as treating diabetes), medical research on *Heloderma* venom has increased exponentially (chap. 3). More researchers have also begun to explore the ecology and physiology of this unique group of lizards. In this final chapter, I'll discuss some of the gaps to be filled in our knowledge of helodermatid lizards and suggest some directions for future research. The ideas mentioned in this chapter are by no means all-inclusive and, in reality, scarcely scratch the surface.

TAXONOMY, EVOLUTION, AND DISTRIBUTION

Because Gila Monsters and Beaded Lizards are members of the clade most closely allied to snakes (the Varanoidea), research on the biology of these lizards can shed light on the evolution of squamates, in general, and snakes, in particular. Since Bogert and Martín del Campo (1956), no one has published a complete morphometric analysis of the Helodermatidae. Researchers today have access to far more specimens (in museums and zoos) than did Bogert and Martín del Campo. Given recent discoveries about the molecular diversity of this family (Douglas et al. 2003), an updated morphometric analysis would be very useful for understanding the relationships among the species and subspecies of the group. In addition, further work on genetic variation in helodermatid lizards is needed, both within and among populations, for subspecies and species. Such information will be particularly valuable for ensuring the protection of habitats that capture the range of genetic variation that exists in nature.

In some regions, such as Arizona, populations of *H. suspectum* are more widely distributed through the landscape. This is likely in response to the more widespread dispersion of suitable Arizona upland and semidesert grassland habitats. In other parts of their range, such as the Mohave Desert in southwestern Utah and southern Nevada, Gila Monster populations appear to occur in pockets of relatively high density (at least historically) separated by vast areas apparently devoid of the lizards. Whether these patterns are mere perceptions or real features of the distribution of these lizards needs to be further explored.

THE VENOM SYSTEM

The functional histology of the venom gland and the mechanisms of venom production in helodermatid lizards remain poorly understood. It is somewhat surprising that no work on these topics has been published recently, despite considerable interest in the biochemistry of helodermatid venoms. Two very different categories of compounds—kallikrein-like peptides that produce great pain and inflammation, and biologically active peptides that produce few toxic effects—are produced in the venom glands (chap. 3). These two groups of peptides/proteins seem to play different roles. The defensive role of the kallikrein-like toxins seems obvious. On the other hand, although many of the bioactive peptides produce spectacular physiological responses, they are not particularly toxic. As mentioned in chapter 3, exendin-4 increases 30-fold in the blood of *H. suspectum* immediately after a meal (Young et al. 1999a). It seems plausible that the exendins may play a role in the digestive physiology of helodermatid lizards. Research into what this role is, and the mechanisms underlying it, could enhance our understanding of digestive physiology in not only reptiles but other vertebrates as well.

What constitutes *venom*, and what constitutes *saliva*? Are different venom constituents produced in different regions of the glands and in response to different stimuli? The venom glands of helodermatid lizards are modified salivary glands (chap. 3). Interestingly, salivary glands and the pancreas emerge from the same tissue early in their embryonic development and many of the bioactive peptides are basically pancreatic secretagogues (Raufman 1996). Research on the form and function of the venom/salivary glands of helodermatid lizards, and the physiological role of the bioactive peptides they produce, would be a fruitful endeavor for the future.

Snake venoms show considerable geographic variation, some of which may be in relation to diet (Daltry et al. 1996). It is likely that genetic variation among subspecies or populations of helodermatid lizards may result in differential expression of peptides within the venom. There is some evidence that this occurs and that the venom of *Heloderma* shows geographic variation. For example, the abundance of helospectin in the venom of *H. suspectum* seems to vary, possibly in relation to commercial sources from which the samples are obtained (Raufman 1996), and venom LD_{50} values vary from lot to lot. This phenomenon has not been carefully investigated but would be a fruitful area for future research. In some vipers, the venom undergoes ontogenetic changes associated with dietary shifts as snakes mature (Mackessy 1988; Andrade and Abe 1999b). One way to test the hypothesis that *Heloderma* venom plays a feeding role would be to explore this phenomenon in Gila Monsters and Beaded Lizards. If venom serves a more important feeding role for juvenile than for adult *Heloderma*, one might expect ontogenetic changes in the chemistry of *Heloderma* venom as well. It is often assumed that snake venoms aid in predigesting prey, yet this phenomenon has been little explored. Studies are necessary that directly test whether digestion is enhanced by tissue-destroying venom enzymes, both in snakes and in lizards. Perhaps even more important will be to explore whether the bioactive peptides in the venom of helodermatid lizards serve as endocrine hormones that act to regulate their own digestive physiology (Young et al. 1999a).

There has been recent interest in how snake venoms vary in relation to diet (Mackessy 1988; Daltry et al. 1996). Another potentially instructive direction might be to investigate how snake venom constituents vary in relation to the importance of that venom for defensive purposes. One might predict that snake venoms that perform important defensive functions (in addition to their role in prey acquisition) would show a greater proportion of components that cause immediate pain.

PHYSIOLOGICAL ECOLOGY

Preliminary evidence that exendin-4 might play a digestive role in helodermatid lizards (Young et al. 1999a) opens the door to a host of other questions about their digestive physiology. Other squamates that experience long intervals between large meals must up-regulate a previously quiescent gut, an activity that requires numerous regulatory peptides and can consume over 24% of ingested energy (Secor et al. 1994; Secor and Phillips 1997; Secor et al. 2001). Do helodermatid lizards exhibit a similar up-regulation of the gut? Does exendin-4, and perhaps other peptides awaiting discovery, mediate this process in some way?

As discussed in chapter 4, the high aerobic capacities of Gila Monsters and Beaded Lizards may be as much a result of selection for endurance during strenuous male combat rituals as they are adaptations for foraging activity. This hypothesis needs to be further tested in varanid lizards, which show a range of aerobic capacities, activity levels, and male–male combat behaviors.

The tail as a potential water-storage organ in helodermatid lizards has not been thoroughly investigated and may prove a fruitful topic for future research on how helodermatid lizards endure periods of drought. The role of the urinary bladder in regulating body water is currently being investigated by Dale DeNardo and his students (pers. comm.). DeNardo and colleagues are also investigating whether high rates of evaporative water loss (DeNardo et al. 2004) allow wild *Heloderma* to reduce their body temperatures via evaporative cooling, or whether *Heloderma* can control rates of evaporative water loss.

HABITAT USE AND ACTIVITY

Shelters may be a limiting resource for helodermatid lizards and perhaps also for other animals inhabiting deserts and dry subtropical environments. The physiological consequences of habitat selection for ectotherms have been recognized for some time (see Huey 1991; chap. 4). A fruitful arena for future research would be the analysis of the roles of subsurface refugia (and associated microenvironments) in the ecology of additional species inhabiting seasonally variable environments. Moreover, a more complete understanding of the ecological roles of the microhabitats of *Heloderma* would help develop a more complete picture of the biological constraints on helodermatid lizards as well as help managers identify and protect suitable habitats.

Humidity (or, more accurately, vapor pressure deficit) is a significant factor in shelter selection by Gila Monsters (Beck and Jennings 2003). Our understanding of microhabitat use by ectotherms has been built largely from studies of the role of temperature and thermoregulation (Porter et al. 1973; Humphreys 1978; Huey 1991; Diaz 1997). The role of humidity in microhabitat selection by desert ectotherms is obviously also an important factor that deserves more attention.

POPULATION BIOLOGY

To understand population trends throughout the range of *Heloderma,* additional estimates of population size (and other population characteristics) are needed. The extent of mortality owing to roads, pets, and displacement have never been quantified. Almost nothing is known about the ecology of juvenile helodermatid lizards. Population characteristics, such as population density, age/size structure, sex ratios, fecundity, and other variables, are difficult to determine for helodermatid lizards, but, in reality, few researchers have attempted to measure these important attributes. Aside from Martin and Lowe's seminal work (chap. 6), few field data exist on population dynamics of helodermatid lizards. As more researchers begin to investigate the various populations of *Heloderma,* efforts must be made to obtain data on population parameters.

How do populations fluctuate over time? If we see ups and downs in the number of individuals of a monitored population, how will we know whether these are signals of recovery, harbingers of a crash, or natural cycles in population density? Better knowledge of the population biology of helodermatid lizards can help us to predict, and hopefully to avoid, widespread declines brought about by the onslaught of human population growth and expansion.

FOOD HABITS

The diet of helodermatid lizards appears to vary among populations. To what extent do differences in diet reflect variation in prey availability? During foraging, Gila Monsters seem to revisit the same foraging areas year after year. What are the signals used by helodermatid lizards to identify favorable foraging areas? Are they chemical cues or spatial cues, or both? Exploring the role of chemoreception and memory in foraging behavior in such a long-lived predator would be a fascinating endeavor.

There is much interest in the functional morphology of the squamate tongue (e.g., Schwenk 1995), yet no one has carefully examined the tongue of *Heloderma.* When eating eggs, Gila Monsters and Beaded Lizards will engulf the entire egg in their mouths then finish crushing the shell as it is swallowed whole. This avoids spilling the precious, high-energy contents. However, some of the eggs that helodermatid lizards eat in nature (e.g., tortoise and chachalaca eggs) are so large that they must be broken before they can be taken into the mouth. Is the flatter, wider tongue of *Heloderma* an adaptation to lap up the spilled contents of eggs (a forked tongue that also acts as a "spoon")? Another interesting question is, why do *H. horridum* have pink tongues and *H. suspectum* black ones?

REPRODUCTION

We still know very little about the nesting biology of helodermatid lizards. Actual nest conditions and incubation periods in nature are still unknown for both *H. horridum* and *H. suspectum.* In addition, the complete reproductive cycle of *H. horridum* still needs to be fully documented (Goldberg and Beck 2001). Within an individual's home range, nest sites may be limited to specific soils that are suitable for digging and that retain humidity and temperature in a way that enhances incubation and development. Such nesting microenvironments may be distant from other areas used for foraging, escaping heat, or overwintering. Research on the nesting biology of helodermatid lizards might help us understand not only their reproductive biology but also the ecological factors limiting their distribution (chap. 2).

CONSERVATION

Conservation biology is perhaps the most important focus for future research on helodermatid lizards. To develop effective conservation strategies for *Heloderma,* we must first determine the current extent of suitable habitat, assess the quality of remaining habitat, and establish priorities for habitat protection given economic and political limitations. We need to do more than protect habitats, however; we need to understand the biological constraints of the species—the suite of resource demands that must be met in a particular habitat (Dodd 2001).

Because helodermatid lizards are rarely active on the surface, it is difficult to conduct population surveys on them. Yet survey protocols are needed to assess the occurrence of sensitive *Heloderma* populations, especially in areas with rapidly expanding human populations. Seasonal and spatial changes in resource demands should be taken into consideration when establishing survey protocol. A habitat model has recently been provided for Nevada (Gienger 2003), which needs to be further tested and developed in other parts of the Mohave Desert and developed for use elsewhere.

What applies to one population may not apply elsewhere, so future research must also explore the extent of variation in a number of ecological factors. With the exception of California, detailed field studies have now been conducted on *H. suspectum* in every state within its range in the United States (Utah, Nevada, Arizona, New Mexico). However, very little has been done in Mexico. Researchers in the United States need to work harder to connect with biologists in Mexico and develop collaborations that can answer some of the questions discussed in this chapter, as well as many other important issues that I may have failed to mention here.

The more we learn about helodermatid lizards, the more we realize that this intriguing group has something to teach us. As ancient members of the clade from which snakes likely arose, they are putting a new twist on what it means to be a lizard. The ecology, physiology, and behavior of the Helodermatidae have helped us refine our thinking about reptilian life in the slow lane. And the venom of *Heloderma* is helping to treat serious human diseases such as diabetes. So we can provide a lot of good answers to those who might ask, "What good is a venomous lizard?"

But valuing a species strictly based on what it can do for people is a dangerous and arrogant attitude. Each species has intrinsic value, just as people do. Perhaps a better question is, "What good are we?" If we blithely allow our activities to continue causing extinctions and to reduce global biodiversity, what value does that have? As habitats and the species they contain become ever more fragmented or disappear altogether, so too are we diminished in the process. We still have much to learn about helodermatid lizards. What lies ahead could be even more interesting than what we've already discovered, but only if we act responsibly to protect their survival.

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