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Abstract.—Wild animals and natural habitats are rapidly being lost because of overpopulation and global climate change. Here I recount some of my own charmed life, including adventures and experiences, and I present some preliminary new data on gender differences in 80 lizard species from 14 different families. In most of these species of desert lizards, females are larger than males but males have relatively larger heads than females. Today's lizard ecologists face impediments and a difficult future in which species and habitats are in short supply. I plan to provide access to my own data as a legacy for frustrated future lizard ecologists. These data are described here and online at A Desert Lizard Data Book for the 21st Century (http://www.zo.utexas.edu/faculty/pianka/Proposal.html).

I was exceedingly fortunate to grow up during the best of times in the 1950s–60s when the human population was still only one-third of what it is today. Back then, you could drive through any small town without stopping. Semipristine natural habitats abounded, lizards were abundant, and no collecting permits were required. Little was known about lizard ecology and funding for research was available. During the last half century, things have gone from great to bad to worse, largely because of human population pressures. People are becoming ever more urbanized and removed from nature. Much of the younger generation doesn't even know what's been lost. Most lay people are anthropocentric and, unlike herpetologists, many see little value in wild animals. As we continue to usurp natural habitats, wild animals must now be protected from us. To do anything with a wild lizard, one must obtain permits and pass muster with animal ethics review committees. Before long, it will be illegal even to touch a wild vertebrate. Like lizards, youngsters who love them face a very difficult future.

Boyhood

Some of the passages presented here have been paraphrased or excerpted from my autobiography, "The Lizard Man Speaks" (Pianka 1994a).

I saw my first lizard when I was about 6 yr old in the mid-1940s on a trip east from Yreka, our hometown in far northern California. It was a gorgeous, green, sleek, long-tailed arboreal creature, an *Anolis carolinensis*, climbing around in some vines. I did my utmost to catch that lizard, but all I got was its tail. I still remember standing there holding its twitching tail, wishing intensely that it was the lizard instead. A couple years later, in the classroom next door I discovered a captive baby alligator. I was transfixed by that little gator and stood by its aquarium for hours on end reveling in its every move. As a young boy, I was destined to become a biologist, long before I had any inkling about what science was. Years later, in graduate school, I discovered the layers in the biological cake, and eventually I went on to earn a Ph.D., and, later, my D.Sc. (see below) as an ecologist.

My hometown, in the shadow of Mount Shasta, was a sleepy little town of about 3,500 people, surrounded by relatively pristine wilderness. My boyhood was rich, replete with the great outdoors and lots of adventure. It was an easy walk out our back door to a variety of undisturbed natural habitats. After school, my brother Mike and I roamed the juniper-covered hills around town catching snakes and lizards. We lived outside and knew virtually every hectare within several miles of town. I collected everything from rocks to insects (especially butterflies) to bird eggs to lizards and snakes, including rattlesnakes, with every specimen labeled with its scientific name. I built a glass display case to house my collection of bird eggs, and we went to great lengths to find the nests of all the local species, ranging from hummingbirds to great horned owls. I kept snakes and lizards alive, and when they died, dutifully preserved them as proper museum specimens.

In 1952, at the lucky age of 13, I blew myself up with a dud bazooka shell (Pianka, 1994a). It tore away the middle section of my left tibia and left me with a shortened, partially paralyzed left leg. Many of my young teenage years were spent in hospitals getting bone and skin grafts. Despite my injuries, I have put a lot of miles on my game leg and I have lived a privileged life.

As a sophomore in high school, a plump gimp on crutches, I joined the American Society of Ichthyologists and Herpetologists as a life member for $100. All through high school, I had nurtured a dream, a plan for the future. When I graduated, I was going to take my brother Mike (he was my "legs") and go to Mexico to catch snakes and lizards. My parents humored me along in this fantasy, probably thinking that it would never come to be. But I persisted, and planned it all out. Besides typing, Spanish, and English, the most important class I took in high school was auto shop: my class project consisted of overhauling the engine in my old brown 1948 DeSoto (auto mechanical skills should be a prerequisite for anyone who plans to survive fieldwork in remote areas). I worked and saved every cent I could for the trip.

After graduation from high school in early June of 1956, Mike and I set out for Mexico. He was 15, and I was 17, on crutches, and in a leg brace. We were both exceedingly naive. I wanted to catch a wild boa constrictor and an iridescent blue *Morpho* butterfly. Mike wanted to buy, and explode, fireworks. Armed with our father's Standard Oil credit card (gasoline was 25¢/gallon then), we had about $200 in cash plus a letter of consent from our parents. Would anyone even dare contemplate allowing teenagers to undertake such a trip today?

This was when I discovered deserts—vast, magnificent, uninhabited, and unfenced stretches in Nevada, Arizona, and northern Mexico. Galloping along over the sagebrush to get a lizard jar from the car, I put a crutch down on a Prairie Rattlesnake. When it buzzed, even on crutches, I jumped sky

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high. Over a 2-mo period, we traveled some 9,200 miles through 10 states in the United States plus another 10 states in Mexico. We drove to Mexico City, where we caught turista and witnessed a genuine bullfight, then went south another 200 miles, on to Veracruz. We never found a boa constrictor but my brother did manage to capture one of those strong, fast flying morpho butterflies. (Listen to an online interview with Adrian Smith.; http://www.aodpod.com/5-eric-pianka/).

On our return trip, we rented a rowboat in Louisiana and looked for a wild alligator, but all we caught were some *Anolis*. Two policemen stopped us, wondering what two kids were doing driving a car with California plates over 1,000 miles away from home—they would have taken us in if we hadn't been able to produce that letter giving us parental permission. When I told them I was looking for water moccasins, they looked at one another and then at me like I must be crazy. Driving through Missouri, Kansas, Nebraska, Wyoming, Utah, and Nevada, we saw Yellowstone National Park and the Great Salt Lake. By now, I could hobble short distances without my crutches using a cane. We stopped at every roadside snake pit and snake farm. At one such place, a pair of cobras were in an unattended and unlocked cage—I opened the cage and prodded them with my cane to get the snakes to hood. It frightened Mike, but I found it thrilling. At long last, we returned to Yreka, more mature, well-traveled, wiser, but flat broke. I had to sell the trustworthy old DeSoto for a mere $100 before I set off to college.

College and Graduate School

During the summer between my sophomore and junior years, I made a second trip through Mexico all the way into Guatemala. On that 6-wk journey, I collected snakes and lizards, most of them road-killed animals. During my junior year, I published my first scientific paper, a brief note describing that Mexican collection (Pianka and Smith, 1959). At that time, my life's goal was to write a definitive book on the reptiles of Mexico (such a book is still much needed).

When I first began studying desert lizards as a graduate student at the University of Washington in 1962–64, permits were still not required to conduct field research, and lizards were very abundant at a dozen study areas I worked from southern Idaho to Sonora, Mexico. This gradually changed with the encroachment of urbanization, grazing, agriculture, and land speculation. By the next decade, unfenced desert had become very hard to find. I have returned to Mojave and Twentynine Palms in California and Casa Grande in Arizona to find nothing at study sites that were once teeming with lizards. Two sites in northern Mexico have succumbed to agriculture, indicating a likely reduction if not extirpation of native lizards. Specimens I collected a mere 50 yr ago, safely ensconced in the Los Angeles County Museum, now represent fossil records of what was once there before humans usurped the habitat (Pianka 1994a). Human populations have more than doubled during the past half century—we already use over half of the planet's land surface and more than half of its freshwater. Our voracious appetite for energy, land, water, and other resources continually encroaches on the habitats of all our fellow Earthlings, including lizards (Pianka 2012), with consequences I could never have imagined in those early days

After taking a battery of qualifying exams in graduate school, I discovered a paper on bird species diversity and foliage height diversity (MacArthur and MacArthur 1961) that piqued my interest in species diversity: why are there more species in some places than in others? A prominent geographical pattern, repeated in many different groups of plants and animals, became the focus of my research: latitudinal gradients in species diversity (Pianka, 1966a). I chose to study the ecology and diversity of desert lizards in western North America along a 1,000-km latitudinal transect from southern Idaho through southern Arizona. For three field seasons, I drove up and down this transect collecting lizards. Species richness of lizards living together in flatland desert habitats varied from 4 species in northern cold shrubby deserts to as many as 10 species in the southern warm Sonoran Desert (Pianka, 1967). North American lizard species used two distinct modes of foraging: sit-and-wait ambush vs. active widely foraging (Pianka, 1966b).

I spent the spring of 1966 driving brutal dirt roads half the length of Baja California with my then newly wed wife Helen (now my ex). Baja was then a real wilderness area with no paved road. We censused lizards on low shrubby flat desert areas, comparable with sites I had studied earlier farther north. A flatland desert site in Baja, structurally comparable with my study sites in the Great Basin, supported five different species of lizards. At any given site in North American deserts, the exact number of lizard species present varies from 4 to 10 and depends primarily on the structural complexity and spatial heterogeneity of the vegetation (Pianka 1966b, 1967). After defending my thesis in late 1965, I moved on to a postdoctoral fellowship.

Postdoctoral Days in Australia

While working on my Ph.D., I conceived of an ideal follow-up research project: to compare an independently evolved desert-lizard system with the one I had just studied. I had already begun to dream about the possibility of one day emigrating to Australia, and so it was natural to propose a comparison of Australian desert lizards with those in North America.

I expected to find similar patterns in Australian deserts. I was especially interested in making detailed comparisons of so-called ecological equivalents, independently evolved lineages that occupy roughly the same ecological roles on different continents. A prime example would be North American Horned Lizards (genus *Phrynosoma*), which are in a different family from their Australian counterpart, the Thorny Devil (*Moloch horridus*). Such products of convergent evolution are of special interest to biologists because they suggest that natural selection favors predictable responses to particular environmental exigencies. Moreover, the existence of such convergent species pairs indicates that evolutionary pathways can be predictable and repeatable. I had hopes of not only documenting such evolutionary convergence in detail, but also perhaps contributing new ideas about the vital process of natural selection itself.

I applied for, and was awarded, a 3-yr stipend as a National Institutes of Health postdoctoral fellow to work with the world's leading ecologist, the late Professor Robert H. MacArthur, at Princeton University. Upon finishing my Ph.D. in 1965, I went to Princeton, where I stumbled into a most fortunate interaction. This brilliant ecologist was virtually without any colleagues, extremely approachable, and actually eager for interaction and intellectual stimulation. We began discussing his newest ideas, then just a germ, on costs and benefits of various foraging activities, which led to a classic coauthored paper on optimal use of patchy environments that was seminal in founding the discipline of optimal foraging (MacArthur and Pianka, 1966). At Princeton, I also wrote a companion proposal to support fieldwork in Australia (this was also funded, for MacArthur agreed to be a co-principal investigator).

Soon after, Helen and I boarded a German freighter, aptly named the *Cap Finisterre* ("end of the earth"), and sailed out under the Golden Gate and across the Pacific on our great adventure down under. Going by ship enabled us to take much more luggage than we would have been allowed if we had flown. Everyone should undertake such an ocean trip, if for no other reason than to gain an appreciation for the vastness of planet Earth. Flying fish sail through the air between waves, occasionally landing on the pitching deck. The huge ship dips and climbs waves the size of small hills. Water crashes over the bow. Each noon, the ship's navigator shot the sun's azimuth with his sextant (this was before global positioning systems) and plotted with a colored pin his estimate of our exact position on a huge map of the Pacific posted on the wall in a central social area outside the dining room. We crept slowly across the vast ocean and finally made port in Sydney, a full 3½ wk after departing from San Francisco. I got seasick but found my sea legs and did not suffer jet lag.

Upon arrival in Australia, the entire ship was placed under quarantine until everyone aboard passed health inspection, where they were looking especially for smallpox. Australia had no rabies or hoof-and-mouth disease then, and authorities do their best to keep such fatal diseases off the island continent.

Two of the biggest challenges down under are understanding what is being said to you and learning to respond appropriately: gasoline is petrol, being ill means that you're crook, and if you want to be sure your car has oil, check under the bonnet. Beyond such language "barriers," basic safety requires some retraining: one needs to look right instead of left when crossing a street, and you have to remember to stay on the "opposite" side of the road because Australians, as a reminder of their British roots, drive on left-hand side of the road. I nearly killed myself after changing continents.

We loaded up our Land Rover "Matilda," ordered on an overseas delivery plan from the factory in the United Kingdom, and headed for the great Australian deserts. We did not find many lizards on that first trip across the continent, but we did see kangaroos and a few wombats, plus lots of beautiful birds. In the center of the Eyre "highway" (a rutted muddy track in 1966), I was pleased to find a live death adder, an elapid snake ecologically equivalent to vipers and pit vipers, but a fixed-fang snake related to cobras (this proved to be the only death adder I would see in 7 yr in the Outback).

When we arrived at the University of Western Australia in Perth, we were already becoming relatively seasoned bush travelers. My Australian mentor, Professor A. R. Main, cautioned me that what I wanted to do would be extremely difficult, if not impossible. He gave me valuable advice about traveling in the Outback, such as to carry lots of spare parts, an air compressor, and a high-lift, long-handled "wallaby" jack to get out of muddy bogs. The curator of herpetology at the Western Australian Museum, the late Dr. Glen Storr, suggested taking shovels and a rake. Storr explained to us the art of finding nocturnal geckos using headlights to detect the faint glow of their eyeshine and other techniques for acquiring hard-to-collect lizards.

Handguns are not imported into Australia and cannot be purchased there. Because .22-caliber revolvers were going to be essential for my research, I was advised to bring them with me, and apply for special dispensation. The weapons were seized by customs upon arrival. It took some doing, including letters from Professor Main explaining that handguns were essential for specimen collection, especially wary *Ctenotus* skinks, but the authorities finally allowed me to license two revolvers to be used only in the Outback. I also had to register spring-loaded BB guns classified as air rifles. In contrast to the firearm licensing ordeal, lizards could be collected without any permits back then. I shipped the results of a full year and a half of intense fieldwork (1966 to 1968)—a large crate of preserved lizards from Western Australia—to myself in the United States without any red tape. These specimens are lodged in the Los Angeles County Museum of Natural History.

When I returned to Australia a decade later, I encountered many new impediments. Shipping anything out of the country now had to be approved by federal government officialdom. I also met with stiff opposition from Western Australian police when I tried to license revolvers for a second time, but was again allowed to have gun permits but only on the condition that they were jointly licensed to the Conservation and Land Management (CALM) governmental unit and kept locked up in a secure safe when not in my possession. Moreover, a permit from CALM was required to collect lizards and specimens were to be lodged in the Western Australia Museum.

On each of six subsequent expeditions down under in 1989–90, 1992, 1995–96, 1998, 2003, and 2008, bureaucratic red tape has grown relentlessly, including the formation of animal rights committees. Initially, permits were issued in-house by CALM, but with each trip they were expanded until eventually the animal ethics committee consisted of about 20 people, including lay people and a veterinarian. One asked me "How does killing a lizard help its species?" The last time I stood before this large committee, requesting permission to collect everything I could, I had two copies of our "Lizards" book (Pianka and Vitt, 2003). I opened both to the page with my food web for 40+ species of Australian desert lizards and sent them right and left around the big table explaining that even this enormous compilation was incomplete. The committee conferred and granted me a permit without limits. I was also required to get a "vivisectionist's license" and a poison permit. In Queensland, in 1996, I collected tissues of *Ctenotus* skinks for DNA sequencing. Authorities in that state used the number of specimens in the Queensland Museum as estimates of abundance and imposed strict limits on numbers of putative "rare" species that could be collected, exactly the opposite of what was needed.

"Adequate" sample size depends on who you ask and what you want to do with the data. Our first paper on Thorny Devils (Pianka and Pianka, 1970) was based on a sample of only about 100 individuals. One reviewer, in contrast to permitting committees, complained that was not enough lizards. On the other hand, some Australian biologists have complained about large samples, "Did Pianka need to collect 100 *Moloch* just to show that they eat ants?" An Aussie returned from the desert without seeing many lizards and complained that "Pianka had collected them all." Of course, this was absurd. From my collected specimens, I showed that *Moloch* eat ants, but I also exploited this sample to evaluate reproductive and fat body cycles as well as sexual dimorphisms. Large enough samples over time can yield invaluable information on growth rates and longevity. My collections were well off road and in the vast Australian desert could be compared with a pinprick on the back of a whale. We biologists identify each individual and give it a unique number before preserving it for posterity in a museum. Compare our trivial efforts with those of a mining operation or a developer leveling square kilometers of habitat, keeping no record at all of what has been destroyed.

Once all the bureaucratic hoops were successfully navigated, the lizards present their own unique challenges. Locating most species of lizards down under requires considerable expertise in stalking and tracking. I have frequently worked all day long for 10 specimens, sometimes even fewer. Guns proved to be relatively useless with many wary skinks, requiring development of new techniques such as "whomping." We coined this term for flattening spinifex tussocks with the broad side of a shovel. If the lizard darts out, you whomp the tussock it runs to, and so on. Sometimes a lizard is squashed flat, but very often a nearly perfect specimen results. Although this technique produced specimens, both Helen and I injured our lower backs in its application. We had to do a lot of digging for lizards, too. After a whomp, if no lizard appears in the spinifex, one must dig out the burrow systems underneath the tussock. Sometimes you get a lizard you didn't even bargain for. Helen and I discovered seven new as-yet-unnamed species of *Ctenotus* skinks in 1966–67, one of which was christened *Ctenotus helenae* and another named *Ctenotus piankai* by Storr (1968).

Other species of lizards could only be collected by digging up their burrows. We moved truckloads of sand, and literally wore out shovels in such activities. A large nocturnal skink, *Liopholis striata*, one of the few skinks that has evolved elliptical pupils, digs elaborate tunnel systems that are used as retreats by many other species of reptiles. These complex burrows are an important feature of the Australian sandy deserts, with several interconnected openings often as far as a meter apart, and up to half a meter deep, reminiscent of a tiny rabbit warren. Most of the sand removed from a *L. striata* burrow is piled up in a large mound outside one main entrance. We excavated hundreds of these burrows by covering all but one entrance, digging a steep-sided pit for that entrance, then attacking the other entrances. We had to be ready to pounce. It is rather disheartening to lose a lizard after spending three-quarters of an hour working up a sweat moving a large wheelbarrow-load of sand. It is always wise to check all such pits the next day, as sometimes lizards or other creatures appear in them (this is how we collected our first small marsupial mouse, an undescribed genus in 1967, now named *Ningaui*). You must remain cautious when digging out burrows, for sometimes they contain large venomous elapid snakes.

Finding geckos at night by their dim eyeshine is tricky. You have to be looking from just the right distance away. Too close or too far, and you simply cannot see geckos. Spiders and certain insects also have bright sparkling eyeshine, and since these are plentiful, one must learn to ignore them but perceive and distinguish the much fainter eyeshine of geckos. Helen proved to be an excellent geckoer; night after night, she would return with two to three times as many as I could. She enjoyed geckoing, likening it to an "Easter egg hunt."

One of the hazards of geckoing is getting lost—it's easy to lose your bearings at night, and I have had several close calls when it looked as if I would have to spend the entire night out in the cold desert (5°C, ∼ 40°F). I started to leave a light shining at camp to help find our way back, but this failed when one got a little too far away or the bulb burned out or the wind blew the light over. Finally, I constructed a proper fail-safe 12-V "beacon" with dual red and green lights that could be clamped high up on a tree or radio antenna fitted with long leads to reach the car battery.

Burning a large clump of spinifex is another way to obtain some species of lizards that are exceedingly difficult to collect because they seldom leave these tussocks; the spinifex-dwelling gecko *Strophurus elderi*, a cryptic skink called *Cyclodomorphus melanops*, and the flapfoot legless *Delma* (pygopodid lizards) were collected this way. One must stay by the burning spinifex with a shovel, ready to pounce or shoot, and afterward, it is wise to scrape away the ashes and dig up the burrows beneath the tussock; occasionally, one finds a lizard that has been killed by the heat. However, because a burning fire might escape and set fire to the whole desert, I burn spinifex only when winds are relatively calm (infrequent in the desert).

In my old age, I have come to rely on a more passive, but powerful, technique to capture many kinds of lizards: pit trapping with drift fences. At a reasonably good site, each such trap in an arrangement will yield a lizard every few days. With dozens of traps, a fair sample can be captured. Such a trapline is expensive and time-consuming to set up, requires regular checking to avoid trap deaths, and, in Australia, kangaroos regularly punch holes in drift fences with their toes when hopping cross-country.

Major advantages of pit trapping are that lizards are captured alive and undamaged, and rare and uncommon species that are exceedingly difficult to capture in other ways fall into pit traps. Trapping success can be expressed in lizards per trap day, facilitating comparisons of relative abundances between sites because the common method of collection provides a standardized unit of measurement. However, pit trapping has numerous disadvantages: traps tie you to one spot; no data are collected on precise time of activity, body temperatures, or microhabitat; and some species are adept at avoiding pit traps. In addition, ants are extremely plentiful in Australia, and they frequently mass at a pit trap. A swarm of ants can completely dismember a small lizard and carry it away in pieces within a few hours. Other lizard predators, including foxes, monitor lizards, snakes, and certain birds, learn to raid traps.

Getting stuck in mud is another hazard. Most of Australia is fairly flat. Precipitation is scant and exceedingly variable, but sometimes falls in massive amounts. When a heavy rain finally does arrive, runoff is limited by the restricted topographic relief, causing low-lying areas to become shallow lakes. Such places quickly turn into treacherous muddy bogs, which can stay that way for a long while afterward, even after the surface dries out again. In such a situation, one can pull off the track to camp for the night, with everything looking just fine, and then awake in the morning only to find that the car has broken through the thin dry surface crust and sunk down into underlying mud up to its floorboards. Many tracks are cut below the surface and thus become impassable during "the wet." Frequently, detours around the lowest spots are marked with rough signs. Drainage ditches cut in along the edges of roads become mud traps. Nothing is much more pathetic than a sturdy four-wheel drive helplessly mired up to its axles in bottomless mud, like a dead elephant.

The first few times this happens, you think that you'll never get out. We always seemed to get bogged in really remote places where one could wait for months before anyone else might happen along. I have of necessity gained considerable experience extracting vehicles from bogs (more than I would like). To avoid getting bogged, one should always try to steer away from the edge of the track (this, however, is not easy, since a vehicle slides on the slippery mud and gets pulled sideways toward and into the softer shoulders of deep mud). Don't try to drive around puddles if this means you have to drive on the edge of the track—the hard-packed wheel ruts in the center of the track are usually safer than the unpacked edges. Once bogged, do not simply put it in low range, and spin the wheels, as this will just dig the car in deeper. Even if you have a strong winch, the first thing to do is to unload the vehicle — it's hard enough to get its own weight out, let alone a massive payload. Carry the contents forward to high, dry ground where you will reload them after getting unbogged. One side is often deeply mired, whereas the other side still remains on fairly firm ground. If so, do not try to dig on the mired side, but instead get out your high-lift jack, and some sort of large block, and lift the stuck tires, one by one, up as high as possible. Fill in underneath them with rocks, if possible (otherwise, use sticks and logs). Then, drop the car down, and repeat.

When winter came and lizarding got slow, we decided to take a trip up to the warmer tropics. I had always wanted to cross the "dead heart" of central Australia, but so far we had merely skirted the edges and made limited forays out into it. Obtaining permission to travel through the large central Aboriginal reserves, we topped up fuel and water in Laverton, and set out for Alice Springs, via Warburton. A road sign said "Caution: No Fuel or Water for 570 km—Obtain Supplies in Laverton."

Grinding along on this little-used track, our Land Rover suddenly died, stopped dead in her tracks with both tanks full of fuel. High school auto shop to the rescue: 1) Check carburator to see if the engine is getting gas, yes. 2) Check to see if a spark is reaching the plugs, no. 3) Look around to determine why not . . . notice that the throttle linkage has been rubbing against the main ignition cable from the coil to the distributor, has worn through the insulation, and the spark is grounding out before reaching the distributor. Solution: wrap ignition cable in electrical insulating tape, and secure it away from the throttle linkage apparatus. Five minutes later we're on our way again, just a little scare.

University of Texas

After 18 months of intense fieldwork, Helen and I returned to Princeton in 1968 where I began analyzing data and writing scientific papers about Australian desert lizards. In August 1968, I became an assistant professor at the University of Texas in Austin (where I am now an endowed professor).

A decade later, in June 1978, I returned to Australia to resume studies as a Guggenheim Fellow. My goal on this second trip was to study just two sites but this time in as great detail as possible so as to better characterize uncommon species (understanding rarity is a major challenge in ecology). I chose to continue to study one of my earlier sites, the L-area, about 40 km east of Laverton (Pianka, 1969). This site was accessible and was the type locality of half a dozen new species we had discovered in 1966–67. At this time I first established Red Sands as a study area. Working hard from June through early December, my assistants and I collected about 40 species of lizards at Red Sands (the count is now up to 55 species).

Kalahari

During 1969–70, I extended my intercontinental comparisons to include the Kalahari semidesert of southern Africa. With the able assistance of my good friend and colleague Ray Huey, I was extremely fortunate to be able to extend my intercontinental comparisons to include a third independently evolved desert-lizard system. In terms of its climate and physiography, the Kalahari is virtually identical to the Great Victoria Desert in Australia. Both areas have summer rains, and stabilized long red sand ridges running parallel to the strongest prevailing winds. Indeed, without their characteristic plants and animals, one would be hard pressed to distinguish between these two regions on the basis of physical environments alone. Their biotas, however, are very different. Large ungulates abound in the Kalahari, including Steenbok, Springbok, Gemsbok, Hartebeest, Eland, and Wildebeest. These in turn support many large and small predators, including Lions, Leopards, Cheetahs, Hyaenas, Jackals, Bat-eared foxes, Mongooses, and suricates (Meerkats). Most lizard families are shared (Agamids, Geckos, Skinks, and Varanids), although a few differ (Pygopodids in Australia, Chameleons and Lacertids in Africa). Species richness of lizards in the Kalahari is only about half that found in Australia but almost double that of North America (Pianka, 1971).

I was surprised to find that closely related Kalahari Lacertids differed in foraging mode; Ray and I pioneered methods for quantifying modes of foraging and summarized ecological correlates of foraging mode (Huey and Pianka, 1981). The literature on animal foraging was reviewed by Perry and Pianka (1997) and Perry (1999), and elevated to a paradigm in a 2007 book (Reilly et al., 2007) with a preface by Huey and Pianka (2007) and a chapter by Vitt and Pianka (2007).

Intercontinental Comparisons

I have spent the last half century collecting extensive data on ecological relationships of lizard faunas at some 32 desert study sites at similar latitudes on three continents: the Great Basin, Mojave, and Sonoran deserts in western North America, the Kalahari Desert in southern Africa, and the Great Victoria Desert in Australia (Pianka, 1973, 1985). Lizards have evolved in response to desert conditions independently within each of these continental desert systems. North American flatland deserts supported from 4 to 10 lizard species, Kalahari sites had from 11 to 17 species, whereas Australian study areas had from 15 to 55 species.

A major virtue of these data is that identical methods and resource categories were used by the same investigator for each of three continental desert-lizard systems, enabling meaningful intercontinental comparisons. This unique body of data has thus allowed detailed analyses of resource utilization patterns and community structure in these historically independent lizard faunas (Pianka, 1973, 1986).

Proportions of total species utilizing various foraging modes differ among continents: a full 60% of North American lizard species are sit-and-wait ambush foragers, compared with only 16% in the Kalahari, and 18% in Australia. Percentages of active widely foraging species are 14% (North America), 27% (Kalahari), and 36% (Australia).

Diets of desert lizards are dominated by relatively few food types. Prey resource spectra are broadly similar among the three continents, although notable quantitative differences occur. In North America, the seven most important food types (totaling 84% by volume), in decreasing order by volumetric importance, are: beetles, termites, insect larvae, grasshoppers plus crickets, ants, plant materials, and vertebrates. In the Kalahari, just three food categories far outweigh all others (total 71%): termites, beetles, and ants. In Australia, the five most important categories (total 77% percent, in decreasing order) are: vertebrates, termites, ants, grasshoppers plus crickets, and beetles.

TABLE 1. Numbers of sites, species, and individuals collected in various deserts along with years visited.

Desert	Year	No. of sites	No. of species	No. of individuals
Great Basin	1962–64	3	4–5	558
Mojave	1963–64	4	6–8	1,407
Sonoran	1963–69	5	7–10	2,014
Kalahari	1969–70	10	11–17	5375
Australia	1966–68	8	15–39	2,830
Australia	1978–79	2	32–42	3,003
Totals	1962–79	32	4–42	15,187
Desert	Year	No. of sites	No. of species	No. of individuals
Australia	1989–91	2	34–43	3,873
Australia	1992	3	28–33	1,320
Australia	1995–96	2	20–43	2,676
Australia	1998	2	36–37	2,143
Australia	2003	2	33–38	1,435
Australia	2008	2	38–40	1,187
Totals	1989–2008	3	20–55	12,634

Three categories, termites, beetles, and ants, constitute the major prey items in all three continental desert-lizard systems. Termites assume a disproportionate role in the Kalahari, as do vertebrate foods in Australia (largely a reflection of the diets of varanids). Some species have broad diets but others are dietary specialists, especially on ants and termites (Pianka, 1986).

Although a comparison of diets between nocturnal and diurnal lizard species on different continents would be fascinating, disparities among the number of nocturnal and diurnal species found at my study sites would make such comparisons tricky (e.g., paucity of nocturnal species in North America and differences in diet composition between Australia and the Kalahari).

Diets of closely related species differ. We plotted positions in the first two principal components in dietary niche space for four abundant species of *Ctenotus* skinks (Goodyear and Pianka, 2011). *Ctenotus piankai* eats more hemiptera than other species and *Ctenotus calurus* consumes more termites. *Ctenotus quattuordecimlineatus* eats more grasshoppers and spiders, whereas the more generalized *Ctenotus pantherinus* occupies the central part of this dietary niche space. Diets shift in time but each species has its own distinct diet. Each point is an estimate of the realized food niche at a given point in time, whereas the area filled by all data points for each species represents its fundamental food niche. Overlap between species occurs but is limited (Table 1).

Intercontinental comparisons reflect the extent to which interactions between the lizard body plan and desert environments are determinate and predictable. Convergences observed between such independently evolved ecological systems provide important insights into the operation of natural selection and underscore general principles of community organization.

I have amassed a prodigious amount of data over my lifetime. No one is likely to replicate my monumental effort to understand the ecology and diversity of the world's desert lizards. Because such invaluable data may never again be assembled, my data must be preserved for posterity.

From the beginning, my research protocol has been to collect all lizards captured, then dissect them for data on sex, reproductive condition, stomach contents, and body measurements. Early on (1962–79), lizards were hunted and captured during their normal daily course of activity, providing data on time of activity, microhabitat, ambient air temperature, and active body temperature. These data, however, had collector bias and did not provide reliable estimates of relative abundance.

In 1989, I changed my Australian research protocol and since then most lizards have been pit trapped. Although trappability varies from species to species, this technique provides a standardized collecting method that allows relative abundances to be compared across space and time. It also allows informative estimates of point diversity, which can be used to infer habitat requirements.

After spending over a year tracking down and collecting dozens of *Varanus eremius*, I was finally in a position to write a short scientific paper "Notes on the ecology and natural history" of this beautiful little pygmy monitor (Pianka, 1968). I was extremely proud of this little paper, thinking that after all my hard work, I knew more about this varanid species than anyone, except perhaps aboriginals, ever had or ever would. I was rewarded for this effort in an unusual way. During the mid-1970s, our botany and zoology graduate students in population biology founded an arcane club they called the "Darwinian Fitness Club." Customized green T-shirts were made up with the name of the club on the front side, and that particular person's favorite study organism's scientific name on the back side. On the eve of my departure for the deserts of Western Australia for a year's sabbatical as a Guggenheim Fellow, these graduate students held a going-away party and made me an honorary member of their club (the first faculty member to be so honored, presumably because I was a proven "field man"). They presented me with my own customized T-shirt sporting *Varanus eremius* on the back side. I wore this T-shirt with pride down under. Aussies puzzled over it, thinking that it was odd for someone rather out of shape to proclaim publicly to be some kind of a physical fitness buff (of course, Darwinian fitness is simply relative reproductive success).

This varanid species has remained a bit of a talisman for me, and when I submitted my credentials in 1990 to the University of Western Australia for the Doctor of Science degree (not an honorary, but an earned, and reviewed, degree), I had originally planned to submit a collection of about 30 papers on the ecology and natural history of Australian desert lizards. But when I sent my preliminary list to the registrar, she commented that I might want to exclude minor papers published in the Western Australian Naturalist. Because I still considered my short note on *Varanus eremius* to be one of my most important papers, I balked at this suggestion and included this short but important note. My 4-inch-thick D.Sc. thesis contained two books and consisted of five chapters, each its own collection of many papers: 1) General Evolutionary Ecology, 2) Ecology of North American Desert Lizards, 3) Ecology of Lizards in the Kalahari Desert, 4) Ecology and Natural History of Australian Desert Lizards, and 5) Intercontinental Comparisons.

Fire Succession Cycle

Life in terrestrial Australian ecosystems has evolved over millions of years to thrive in habitats kept in a dynamic state through fire succession cycles. Wildfires promote species diversity in plant and animal communities by creating a heterogeneous mix of habitats, each habitat more suitable for particular subsets of species. I documented population and community responses to fire in a species-rich lizard assemblage in the Great Victoria Desert of Western Australia (Pianka, 1996.).

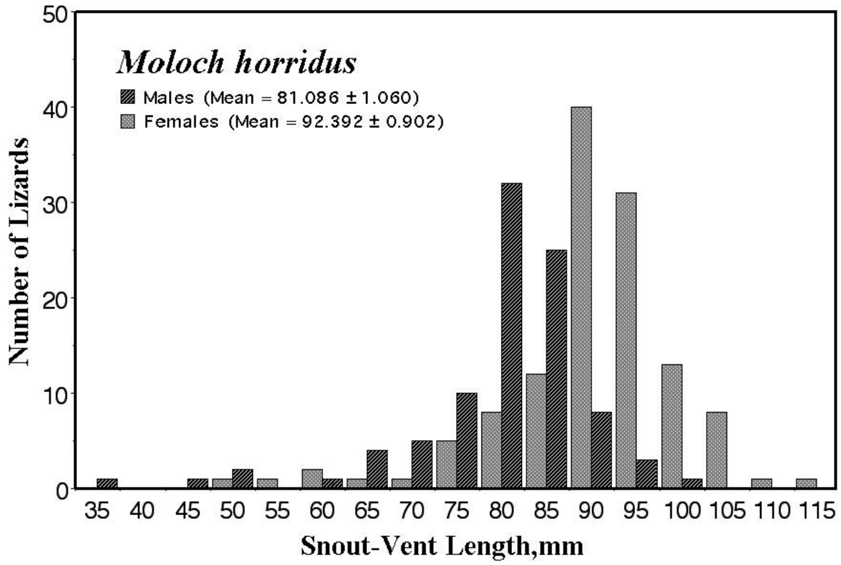

FIG. 1. Histograms of snout–vent lengths of male and female Thorny Devils.

Lizards were censused by pit trapping at a long-unburned flat spinifex site in the Great Victoria Desert in austral springs of 1992 and 1995. A controlled burn was undertaken in mid-October of 1995, and lizards were censused thereafter in late 1995 and early 1996, and then again in the austral springs of 1998, 2003, and 2008 (Pianka and Goodyear, 2012). Forty-six species of lizards (2,872 individuals) were collected and their stomach contents analyzed over the course of a 16-yr fire succession cycle at this single study site. Most strikingly, relative abundances of two species of agamids varied inversely, responding oppositely to habitat-clearing effects of fire. The Military Dragon *Ctenophorus isolepis* reached higher abundances when vegetation was dense, and decreased in abundance in open vegetation after fire. The Netted Dragon *Ctenophorus nuchalis* was rare when vegetation coverage was high but increased rapidly after fire. Abundances of five species of *Ctenotus* skinks, *C. ariadnae, C. calurus, C. hanloni, C. pantherinus*, and *C. piankai*, tracked those of *C. isolepis*. Abundance of a termite-specialized nocturnal gecko, *Rhynchoedura ornata*, increased in abundance after fire. Lizard diets changed during the course of the fire succession cycle, returning to near preburn conditions after 16 yr (Pianka and Goodyear, 2012). In addition to short-term fire succession cycles that contribute to structuring local communities, changes in long-term rainfall also affect desert food webs and regional biotas.

RARITY IN AUSTRALIAN DESERT LIZARDS

Most species of Australian desert lizards are uncommon. I examined possible causes of rarity, including body size as measured by snout–vent length (SVL), fecundity, number of sites occupied, habitat niche breadth, microhabitat niche breadth, dietary niche breadth, and average total niche overlap with other species (Pianka, 2014). Multivariate discriminant function analyses showed distinct ecological differences between abundant and uncommon species. Rare species tended to be larger with lower fecundities than abundant species and they occurred at fewer sites. Many, but not all, uncommon species were specialists, either in habitat, microhabitat, or diet. The niche breadth hypothesis, which states that abundant species should be generalists whereas specialized species should be rare, was tested, but rejected as a general explanation for rarity. Some uncommon species exhibited high overlap with other species, suggesting that they may experience diffuse competition. However, no single cause of rarity can be identified, but rather each species has its own idiosyncratic reasons for being uncommon.

GENDER DIFFERENCES AMONG DESERT LIZARDS

Reporting new data for this perspectives piece was a bit of a challenge, as I have already published hundreds of papers, but there are always new questions to address or new angles from which to view data. Building a vast database has allowed me to connect disparate files so that I can now undertake detailed analyses of sex-specific differences among species, and I present some preliminary results here. My goal is simply to show broad patterns. Male desert lizards differ from females in many ways. Females are often more elusive than males, leading to male-biased sex ratios, especially during the breeding season. In some species, the sexes are similar in size, but in others males are larger than females and in many other species, such as the Thorny Devil (Fig. 1), females are larger than males (Pianka and Pianka, 1970) but males often have relatively larger heads than females (Pianka, 1994b). Testicular cycles correlate with female reproductive cycles, but fat body cycles can differ between sexes (Thompson and Pianka, 1999). In contrast, an examination of thermal biology revealed little difference between sexes (Huey and Pianka, 2007) and use of habitats and microhabitats also seldom differs between sexes, but dietary differences occur in some species.

SEX RATIOS AND BEHAVIORAL DIFFERENCES

Among 11 species of North American desert lizards, sex ratios do not depart from equality except in the teiid *Apidoscelis tigris*, where the ratio is significantly skewed in favor of males (56.34% ± 2.96%). Sex ratios depart significantly from 50:50 in 5 of the 20 Kalahari species, with 3 lacertid species (*Heliobolus lugubris*, *Meroles suborbitalis*, and *Pedioplanis lineoocellata*) biased toward males and two skink species (*Mabuya spilogaster* and *Typhlosaurus lineatus)* toward females.

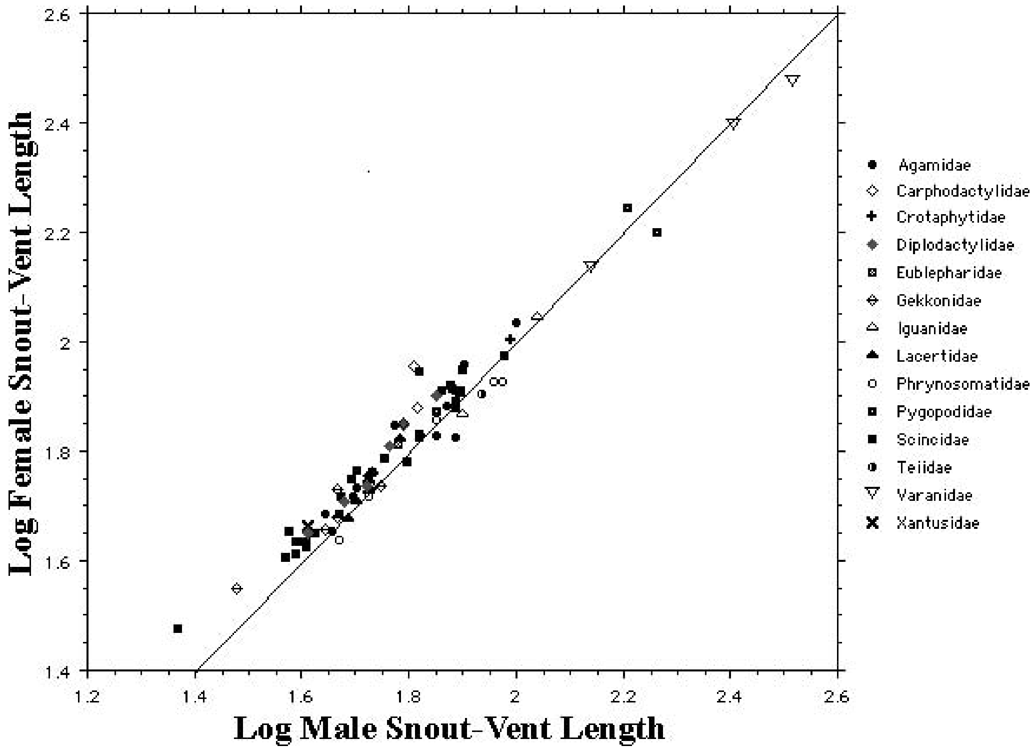

FIG. 2. In most species of desert lizards, females are larger than males. The line in this figure represents the one-to-one line of equal size.

Skewed sex ratios are frequent among 61 Australian species, with significant male dominance in 18 species: 7 species of *Ctenotus* skinks plus 3 other skink species (*Liopholis inornata*, *Lerista desertorum*, and *Morethia butleri*), as well as in 2 pygopodid species (*Delma butleri* and *Lialis burtonis*), 4 gecko species (*Diplodactylus conspicillatus*, *Nephrurus laevissimus*, *N. levis*, and *N. vertebralis*), and 2 varanids (*Varanus eremius* and *V. gouldii*). Among Australian desert lizards, female bias occurs in 2 agamids (*Moloch* and *Pogona*) and in the gecko *Heteronotia*, some populations of which are parthenogenetic.

MORPHOLOGICAL DIMORPHISMS: SVL

Anatomical trade-offs between the sexes are often observed, although their functional significance can remain elusive. In most species, females tend to be slightly larger than males (Fig. 2). The most plausible explanation for this is the fecundity advantage females gain with increased body size. For example, in most lizard species, clutch size increases with body size and females are larger than males (Pianka and Pianka, 1970). Males are larger than females in only a handful of species, perhaps conferring an advantage in male–male combat.

MORPHOLOGICAL DIMORPHISMS: HEAD LENGTH

In most species, males tend to have relatively larger heads than females (Fig. 3), probably because they must fight for females. Such head size dimorphisms occur in most desert lizards I have studied. In only a tiny minority of species do females exhibit proportionately larger heads than males.

As a result, head size dimorphisms are the rule (Vitt and Cooper, 1985). In three species of Australian varanids, *Varanus brevicauda*, *V. eremius*, and *V. gouldii*, heads of males are proportionately larger than those of females (Pianka, 1994b). This is also true for the Kalahari arboreal skink *Trachylepis* (formerly *Mabuya*) *striata* (Fig. 4).

With this brief foray into more recent analyses, I demonstrate that even after publishing hundreds of papers, high-quality data can be used to yield new insights into lizard ecology. Thus, I hope that my enormous data sets will eventually become publicly available, and will be exploited to contribute additional insights into lizard ecology.

CONCLUDING REMARKS

Massive energy consumption by voracious humans has generated huge amounts of waste heat that can no longer be dissipated because of concomitant increases in greenhouse gases, especially carbon dioxide and methane (Hansen et al., 2005). We have warmed both the atmosphere and the world's oceans, which are the major drivers of climate. Climate and weather are driven by these energy gradients.

Because of the vastness and isolation of the Australian deserts, I used to think that Australian desert lizards would be able to persist long after we humans had gone extinct. In fact, I concluded my 1986 synthesis (Pianka, 1986) with the following optimistic statement "Somehow, it is strangely comforting to me to know that, long after we humans have had our day, 40-plus species of lizards will doubtlessly still roam free in the Great Victoria Desert, interacting with one another as they have for millennia, blissfully oblivious of this modest effort to understand those interactions" (Pianka, 1986). But I am no longer so sanguine. The Australian continent is being hit hard by global climate change, specifically El Niño–Southern Oscillation (ENSO) events (Australian Meteorological Bureau, 2015: ENSO website). Historically, interior Western Australia had a low and stochastic annual rainfall of about 150–250 mm and might thus be expected to be particularly vulnerable to the 20–30% decadal

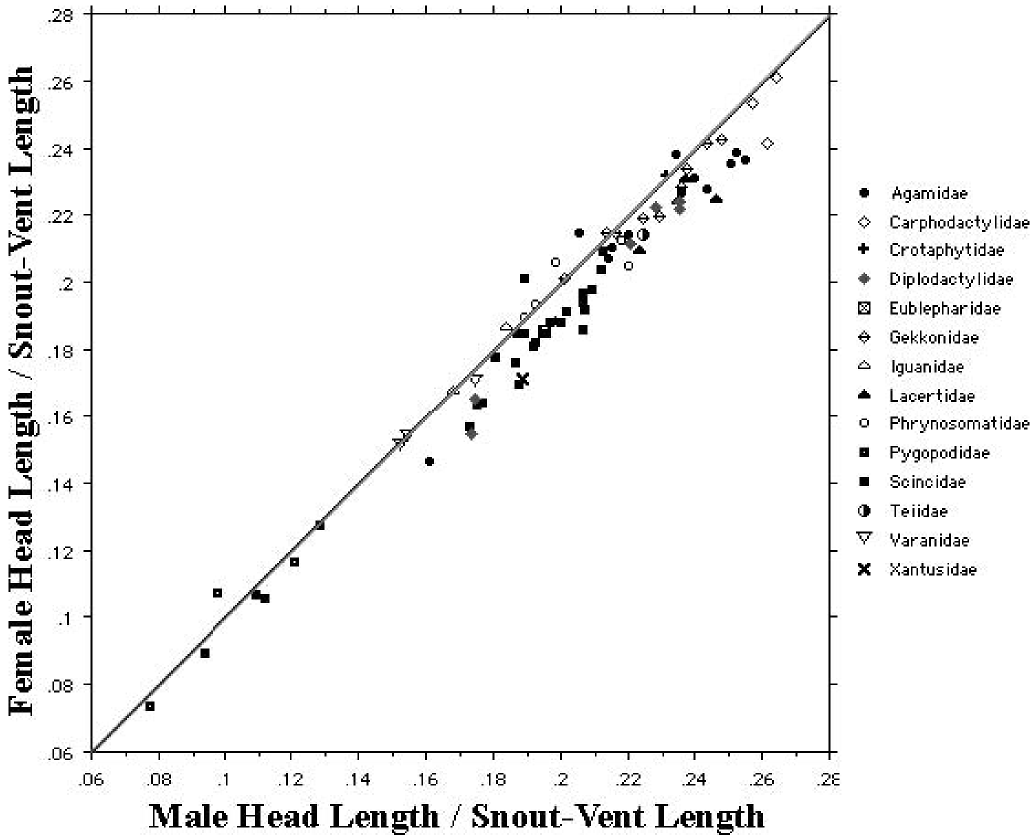

FIG. 3. Mean head size as a proportion of snout–vent length of females vs. males plotted for 80 species representing 14 lizard families. The line in the figure represents the one-to-one line of equal size.

increase in precipitation (Australian Meteorological Bureau, 2015: rainfall trend map). After being away for only 5 yr, I drove right past my long-term study site because the vegetation had changed so much I didn't recognize it. Fires are now much bigger, shrubs are encroaching, and spinifex is declining. These floral changes are affecting the fauna, including insects and other arthropods. Abundances and diversity of their predators, birds and lizards, have declined.

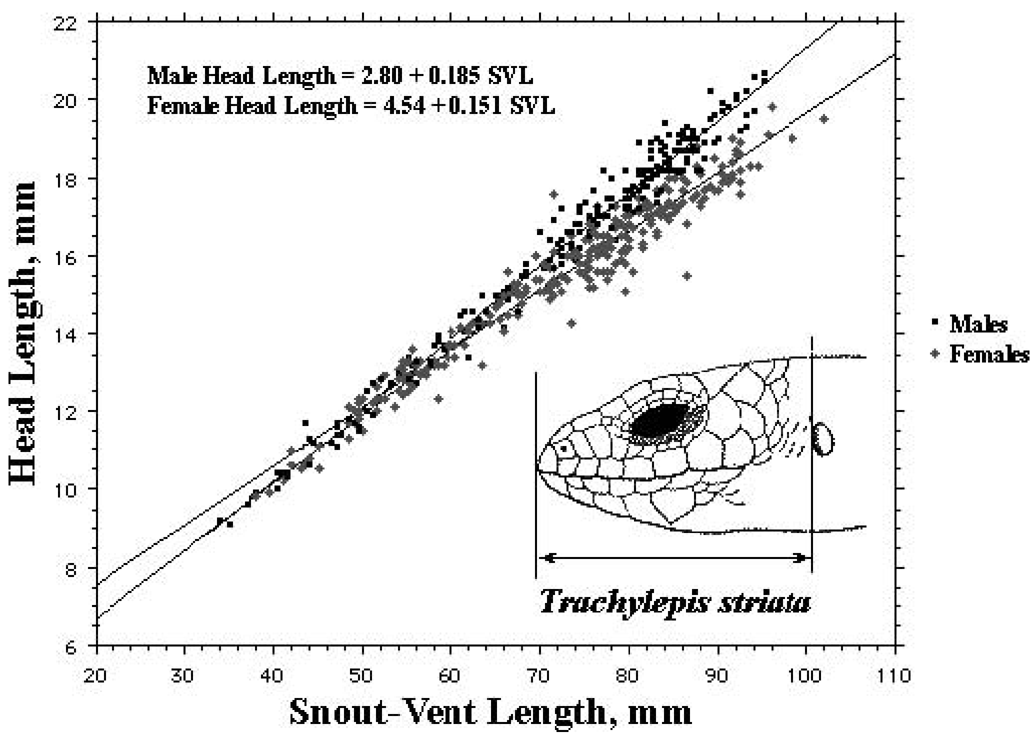

FIG. 4. Head lengths of male (black squares) and female (gray diamonds) Kalahari arboreal skinks *Trachylepis striata*.

Many have expressed interest in my huge unique data set, and I intend to preserve it for posterity with as much information as possible for each individual lizard (almost 28,000 of them). To that end, I have organized these data into a mySQL relational database to be placed in the public domain upon my death (until then, I will continue to mine these hard-won data for whatever they will yield). These data constitute an invaluable resource for a wide variety of future studies, including seasonal and long-term changes, ontogenetic changes, variation and sexual dimorphisms in morphology and ecology (gender differences), microhabitat and habitat requirements, thermal biology, reproductive biology, differences between diurnal vs. nocturnal species, within- vs. between-phenotype components of niche breadth, dietary and microhabitat niche breadth and overlap, and point diversity.

Bottom line: today's youngsters will have limited access to natural habitats, let alone wild lizards. Overpopulation and global warming have become very serious impediments. So, I intend to offer access to my own data as a legacy for frustrated future lizard ecologists.

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