

## The Lizard Kings

Small monitors roam to the east of an unseen frontier; mammals roam to the west

By Samuel S. Sweet and Eric R. Pianka

small lizard, caught in the open, flushes ahead of a pursuing monitor. The prey, desperately seeking escape, begins to run a winding course. The tactic could throw a predator off, but the monitor doesn't bite. Rather than engage in a tail chase, the monitor heads straight for a pile of rocks—the only nearby feature to which the hunted animal could possibly escape. The smaller lizard, outsmarted, arrives at the refuge too late.

Such a display of intelligence in monitor lizards, the animals of the family Varanidae, is not unusual. As a rule, monitors do not have to chase their prey very far, and in many cases they seem to anticipate some gambit by their prey. When arboreal lizards are being hunted and run for a tree, they usually spiral around to the back side to ascend; one of us (Sweet) has watched pursuing monitors of two species (Varanus tristis and V. glauerti), on at least three occasions, spiral around the tree in the opposite direction to catch the prey unawares. (Experienced human lizard-catchers do the same thing.)

The black-palmed rock monitor (V. glebopalma), a three-foot-long lizard from northern Australia, hunts by taking up perches on three- to six-foot-high boulders along the margins of ledges, where it has a good view of some area of more-or-less open ground. If it spots prey-such as, in Sweet's observations, a skink or a frog-it literally projects itself off the boulder, dashes after the prey, and then returns with its quarry at top speed to some rock crevice before doing anything like chomping or whacking the prey and gulping it down. "Lizards" don't do this: if they have something in their mouth, they eat it then and there-no matter that something else may be zooming in at top speed in hopes of a double lunch. But monitors do.

Predators and their prey are locked into a co-evolutionary arms race, in which any advantage gained by one calls for a countermeasure by the other. Less sophisticated, or perhaps just unlucky, prey individuals perish. On average, those with better means of escape survive. More effective escape, in turn, favors predators better able to capture evasive prey, and the bar for both species rises in a reciprocating fashion. Similarly, competing lineages of predators—cats and foxes, for example—are also subject to the Red Queen's dictum that "it takes all the running you can do, to keep in the same place."

A common result of such pressures—less adept animals either don't catch a meal or can't avoid being eaten—is the evolution of larger brains and more sophisticated nervous systems, as well as a potential for increased intelligence. A successful carnivore might have better neuromus-

cular coordination than its peers or its prey; more refined senses (and brain to process the information); or enhanced problem-solving capabilities. Those aspects of neurophysiology co-evolve in turn with ecological and behavioral differences among various kinds of carnivores. The range of possibilities for a predator's behavior—whether it hunts alone or in a pack; whether it lies in wait to ambush or actively chases down its prey; and the degree to which it relies on visual, auditory, or olfactory input to find its meal—all affect the nature and sophistication of the animal's brain.

None of the logic of this arms race leads to the conclusion that effective brains and neural sophistication are restricted to mammals; monitor lizards make that much clear. Superb predators, these animals surpass all other lizards in intelligence. They are alert and agile. Their styles of hunting rely on acute vision and extremely sensitive chemoreception to cover what are typically huge areas relative



Mertens' water monitor (Varanus mertensi) hunts aquatic life in waterways across north central Australia.

to their size. In these and other ways, convergent evolution has led to many similarities between monitors and mammals. Herpetologists have relied on terms such as "mammal-like" and "near-mammalian" so often to describe the monitors that such phrases have nearly become clichés.

The descriptions, however, divert attention from a question that is far more intriguing than mere similarities in habits between the two groups of vertebrates: Are the two groups so similar that they are ecologically incompatible as top carnivores? In other words, does the presence of one group in an ecosystem restrict the presence of the other? An analysis of the capabilities of monitor lizards and small mammalian carnivores, combined with the study of their biogeography, may throw some light on whether, in some ecosystems, the monitor lizards became a fair match for the mammals.

The similar adaptations of monitor lizards and mammalian carnivores are certainly not the products of a shared family history. The most recent common ancestor of the two groups lived more than 300 million years ago. It was a far less sophisticated animal, lacking the metabolic scope, visual and chemoreceptive abilities, and complex information processing that characterize both groups today. Most contemporary features of monitors and mammals that function in similar ways are clearly not the results of similar anatomical endowments.

One substantial difference is that monitors are ectotherms—loosely referred to as being cold-blooded. The more familiar term is something of a misnomer, because the "cold-blooded" monitors, at least, typically operate at tightly regulated body temperatures equal to or higher than those of mammals. Monitors, however, do without the

costly molecular and physiological control mechanisms required by endotherms, the so-called warm-blooded animals. Both monitors and mammals can sustain their activities for long periods.

Monitors do not sense chemicals with the nasal olfactory chamber that is so well developed in mammals. Instead, they transfer compounds from their tongues into two elaborate sensory receptors known as the vomeronasal organs. Vestigial in mammals, these organs occupy paired cavities that open onto the roof of the monitor's mouth.

any accounts of monitors in captivity cite behaviors unusual among reptiles that attest to sophisticated information-processing capabilities. White-throated monitors (V. albigularis) can count up to six. Komodo dragons (V. komodoensis) recognize their keepers. When chasing rats, crocodile monitors (V. salvadorii) anticipate evasive tactics. Few field studies, however, have explored the monitor intellect, and the wariness of monitors in the wild is legendary. But the work that has been done demonstrates that the animals can locate terrain features, mates, and food both by memory and with their

remarkably sensitive chemical detectors.

Monitors are renowned trackers. Alexey Y. Tsellarius of the Severtsov Institute of Ecology and Evolution in Moscow and his colleagues found that Caspian monitors (V. griseus caspius) can distinguish male from female and resident from nonresident monitors merely by sampling their tracks with the vomeronasal organ. If the monitor then gives chase, it unhesitatingly follows the track of the other animal in the correct direction. Our observations in Australia corroborate Tsellarius's finding for both desert and woodland species. One of us (Pianka) once came upon the track of a large monitor known as a

perentie (*V. giganteus*) that had intercepted his own. The track showed that the lizard "ricocheted" off the human footprints and fled in the direction it came from, illustrating its chemosensory talents.

Monitors that feed on the eggs of other reptiles can locate a clutch buried in sloping, backfilled tunnels. They do not gain access via the tunnel entrance, which is often three feet or more away from the eggs; instead, they dig straight down from above. Walter Auffenberg, a herpetologist formerly at the Florida Museum of Natural History in Gainesville, demonstrated that Komodo monitors can detect carrion from nearly seven miles away. Auffenberg also concluded that some monitors climb to ridgelines expressly to sniff the wind for carrion odors over a large area, a foraging strategy that requires substantial planning.

Monitors can apparently recall the positions of refuges within their home ranges. Pianka has observed that such Australian desert species as the perentie and the rusty desert monitor (V. eremius) remember exactly where good burrows are located: the lizards head directly toward them cross-country, which for perenties may be a mile or more. Lace monitors (V. varius) display a similar talent, though put to different use: They lay their eggs in active termite mounds, then return about nine months later to reopen the nests for the hatchlings to exit. Such a feat calls for map knowledge as well as an accurate sense of timing.



With the tongue monitor lizards sample the air for chemical compounds, then transfer the compounds into two cavities that open into the roof of the mouth. The cavities house elaborate chemical sensors called the vomeronasal organs. Pictured here is the common water monitor (V. salvator).

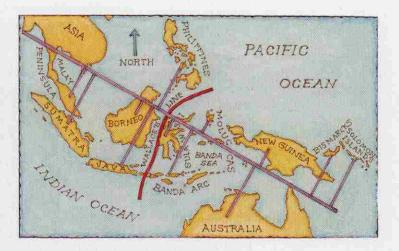
adiotransmitters attached to individual monitors make it possible to follow them closely. We have learned, for instance, that male monitors seek out multiple partners by visiting the home ranges of several females. Sweet observed a male of the small arboreal species V. glauerti descend the

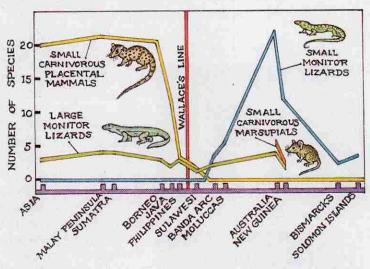
home tree of one female and travel more than 300 yards in a straight line, through dense forest and rock outcrops, to the base of another tree. Six days earlier, he had mated with a second female in that tree, but in the interim she had relocated twice. So, finding no one home, the male trailed her to a third tree fifty yards away, then traveled another seventy-six yards to a fourth tree, where the second female then resided. The entire episode took only forty-five minutes and covered nearly 440 yards in rugged terrain.

This feat called on both mental maps and expert chemical detection. The male was familiar enough with his eighteen-acre home range to make a straight-line return to the second female's old location. Then he tracked her by her odor trail. Each of five male *V. glauerti* studied displayed similar abilities. And Pianka in Australia observed a male of the small arboreal black-tailed monitor *V. tristis* travel 790 yards in a straight line into the wind in one day; it was found in a hollow tree with a female, suggesting that it may have followed an airborne scent trail to find her.

Monitors sometimes adopt unusual foraging tactics. Some semiaquatic species, such as Mertens' water monitor (V. mertensi), use their body and tail to herd fishes into shallow water. The black-tailed monitor has a unique tactic to rustle up skinks, the small lizards on which it feeds. Sweet watched several black-tailed monitors hunting skinks in leaf-filled depressions. The monitors would surge forward under the dry litter and then pop up, holding the head high and ready to pounce on any movement. After a few moments of watching, some individuals abruptly began to twitch and wiggle their tails under the leaves. The twitching sometimes caused a concealed skink to reveal its location.

Many people are familiar with the differences between cats and dogs, as well as between individuals of either group. Similar patterns show up in monitors, both in species and in individuals. During field studies that brought Sweet into daily contact with individuals of several species, he found that some male members of some species became habituated to his presence. Those lizards could be followed closely, and some even climbed onto him a few times. Others, however, became less approachable as his studies continued. Four out of six V. glauerti, two out of forty-two V. scalaris, and three out of twelve V. tristis habituated, whereas each of twelve V. glebopalma and five each of V. scalaris and V. tristis became increasingly wary with time. Either way, the animals clearly recognized and remembered him. Curiously, however, no females of any of these species ever habituated.





Transect line (purple line on map and on horizontal axis of graph) reveals a complementary distribution of species of carnivorous mammals and small monitor lizards. The transect, defined by the authors, makes a roughly perpendicular intersection with a biogeographic barrier first described by Alfred Russel Wallace. Wallace's Line marks the eastern limit of many animals having Southeast Asian affinities, and the western limit of a fauna derived from Australia and New Guinea. On the graph below the map, the number of species belonging to four groups of animals is plotted for various ecosystems that occur along the transect. The graph shows that the diversity of small carnivorous mammals (yellow) and that of small monitors (blue) are virtually mirror images of each other, as if they were reflected across Wallace's Line. The diversity of large monitor species (green) fluctuates randomly across the transect line. The pattern suggests that carnivorous mammals and small monitors may be too similar as predators to coexist, or that the small monitors become prey for the mammals when both are introduced into the same ecosystem. Interestingly, carnivorous marsupials (orange) do not prey on monitors, suggesting that the monitors can outsmart the marsupials but are outdone by the mammals.

None of the complex behaviors we are describing commonly occurs in other reptiles. And certainly no reptiles except monitors have such a broad repertoire of "mammal-like" attributes.

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Throughout Africa and southern Asia monitors coexist successfully with a wide range of carnivorous mammals. The diversity of monitor species on those continents, however, is fairly low, and most of them are large (meaning the adults are more than four feet long) and relatively bulky. Six species occur in Africa and the Arabian peninsula, and one of those extends well into central Asia. Six more species range across mainland southern Asia.

As one moves east, into offshore Southeast Asia, the diversity of monitors increases sharply. Fourteen species are native to the East Indies and the Philippines (four of them also live on the mainland), and sixteen species are native to New Guinea, the Solomon Islands, and the islands of the Bismarck Archipelago.

That high diversity of small monitors in eastern Indonesia and Melanesia has only recently been



Northern quoll (Dasyurus hallucatus; top), a carnivorous marsupial native to Australia, and the masked palm civet (Paguma larvata; above), a camivorous mammal native to Southeast Asia, both coexist with large monitor lizards. Species of small monitors, however, thrive only where the civet and its kin are absent.

recognized. Before 1990 only three small species were known in the region: the widespread mangrove monitor (V. indicus), which varied greatly from island to island; the green tree monitor (V. prasinus) of New Guinea; and V. timorensis, of Timor. Through the efforts of Wolfgang Boehme, a zoologist at the Alexander Koenig Research Institute in Bonn, Germany, and his colleagues, sixteen additional species are now recognized. That work alone has increased the species count of the family Varanidae by about 25 percent. Some of the newly recognized species are local derivatives of the widely ranging V. indicus and V. prasinus; others are more distinct.

The diversity of monitors reaches its peak in Australia, which hosts twenty-seven named species (five are shared with New Guinea) and more than a dozen as yet undescribed species as well. In parts of northern Australia as many as eight or nine species may occur in the same areas, partitioning resources according to differences in body size and habit. One unique and important feature of the Australasian radiation of monitor species is that

more than half of them are small (adults less than four feet long) and of slender build.

To understand why small monitor species have radiated so dramatically through Australia, New Guinea, and their adjacent islands, but not elsewhere, we examined the possible role of Wallace's Line [see map on preceding page]. Alfred Russel Wallace, the nineteenth-century naturalist, did extensive fieldwork in what is now Indonesia, where he noted a sharp dichotomy in fauna between certain islands. One side of the line he traced to mark the dichotomy represents the eastern limit of many animals with Southeast Asian affinities; the other side is the western limit of a fauna derived from Australia and New Guinea.

Wallace's Line is now understood to overlie a region incorporating three major tectonic plates and several smaller ones. Thousands of islands made up of transient volcanic peaks and scattered microcontinental fragments are sandwiched between the eastern edge of the Asian continental shelf and the shelf that encloses Australia and New Guinea. Most important to the biota, no land connections have ever spanned Wallace's Line, and so it represents an absolute limit to the dispersal of organisms that cannot cross the sea. For other species, the line is just a filter, and it is almost irrelevant for many plants or insects that can fly long distances.

The lands in the vicinity of Wallace's Line provide a natural laboratory for testing ideas about the ecological equivalence of mammals and monitors. Virtually none of the small carnivorous mammals of Southeast Asia (cats, civets, mongooses, weasels) have crossed it from west to east on their own. Just one species of civet is native to Sulawesi, to the east of Wallace's Line; other civet and mongoose species in the archipelago were introduced by people.

In contrast to its influence on the mammals, Wallace's Line is not a barrier to monitors—or is it? That depends on the adult size of the species [see lower illustration on preceding page]. Large monitor species (in which adults are greater than four feet long) are just as diverse on lands east of Wallace's Line as they are to the west, or for that matter in mainland Asia and Africa. Small monitor species, however, occur only to the east of the line. Their diversity in that region forms a near-mirror image of the species distribution of small carnivorous mammals to the west. And Sulawesi, the only island east of Wallace's Line that harbors a native placental mammalian carnivore, lacks small monitors.

Did the small monitors, like the small carnivorous mammals, simply halt their radiation at Wal-



Member of the mangrove monitor group (V. indicus and other species) is pictured in New Guinea. The group's domain extends from the islands around the Banda Sea to the Solomon Islands. The indicus group radiated into a variety of habitats; the absence of small placental carnivores has probably facilitated that spread.

lace's Line? Probably not: most monitors are accomplished rafters, and so their distributions probably did not arise from any geographical barrier. Instead, the distributions may have an ecological explanation: the two groups are simply too similar as predators to coexist, and on the landmasses west of Wallace's Line, the small mammals prevailed.

One informative twist on this idea arises in Australia and New Guinea. Many small carnivorous marsupials live there, and some of them—six species of quolls and one phascogale—grow to about the size of civets and mongooses [see photographs on opposite page]. These marsupial carnivores are fierce and agile predators, yet they have evolved and coexist with many species of small monitors.

The behavior of these groups and the ways their ecologies overlap suggest that small monitors are, roughly speaking, "dumber than civets but smarter than quolls." Unfortunately, that simple generalization is being tested by human interventions. Mongooses and civets have been introduced to islands east of Wallace's Line, and foxes and feral cats have been brought to Australia. In a recent field study in northern Australia, Sweet lost thirteen out of fifty-four individual monitors to predation: four were killed by native predators, but nine were taken by a single feral cat. The northern quoll (Dasyurus hallucatus), however, failed to catch any of the monitors.

o complete our story, we must point out that small monitors actually do coexist with small placental mammalian carnivores such as civets and mongooses-in the form of juveniles of the large monitor species! The young of these large monitors are typically highly secretive and often arboreal, but so are many of the small monitor species. Thus, secrecy is not a sufficient explanation for coexistence. We suggest that this coexistence succeeds because large adults can lay many eggs and the young grow quickly; even if many become prey to carnivores, a few will probably reach adult size. Species of small monitors lay fewer eggs, and must spend their entire lives in the arms race with small mammals. Whether they lose out primarily because they become prey, or because they must compete for prey with mammals, remains to be studied.

Wherever monitors live, the arms race has honed their original predatory tool kit. Particularly to the east of Wallace's Line, monitors appear to have achieved striking ecological and behavioral parity with mammals. A century ago the German herpetologist Franz Werner proclaimed monitors "the proudest, best-proportioned, mightiest, and most intelligent of all lizards." We certainly concur, and could add many superlatives to Werner's list. Human beings are fortunate to share this planet with such extraordinary animals, and we should try to learn from them whatever we can.



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