

6 Introduction

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OVIPARITY

One of the great evolutionary steps that gave reptiles their advantage over amphibians was the evolution of the amniotic egg with its protective shell and amniotic membrane. It allowed reptiles to lay their eggs on land, and negated the general amphibian requirement to return to the water to reproduce. Reproduction via external eggs containing under-developed embryos is known as “oviparity,” and the majority of living reptiles are oviparous, for example, all turtles and crocodilians; birds, which are technically avian reptiles; the tuatara; and most snakes and lizards.

Even basal mammals were oviparous, as evidenced today by the monotremes. Of the 42 snake families, 23 are fully oviparous (see Table p.43), with another four oviparous subfamilies in families that demonstrate mixed reproductive strategies.

The shapes and textures of eggs vary greatly within the lizards, but all oviparous snakes lay leathery-shelled eggs, ranging in shape from ovoid to elongate. Many snakes simply lay their eggs in a hidden place where the humidity and temperature are optimal, but eggs laid in this way are subject to the vagaries of the weather and may perish.





LEFT | The baby Burmese Python (*Python bivittatus*) cuts a slit in the eggshell with a special egg-tooth on its front upper lip, but it may not emerge fully for some time as it absorbs the remains of the egg sac.

OPPOSITE | A female Diamond Python (*Morelia spilota spilota*) coils around her eggs, not just to protect them but also to incubate them using “shivering thermogenesis.”

The female Western Grass Snake (*Natrix helvetica*) often lays her eggs in the same suitable location year after year, and several females may use the same site, possibly a warm compost heap in a garden; but even though grass snakes are common in England and Wales, they do not venture very far north into Scotland, the conditions being uncondusive to an oviparous species.

Females of some oviparous snake species are more attentive to their eggs. Pythons will coil around the clutch throughout its incubation, not just to protect the eggs from potential predators, but also to enhance incubation. A female python, a cold-blooded reptile that spends her life at the ambient temperature, can raise her body temperature during incubation by a process known as “shivering thermogenesis,” as waves of rhythmic muscular contractions pass around her body coils, resembling twitching; this muscular

activity raising her body temperature by as much as 13–23 °F (7–13 °C) above the ambient temperature. Defying the definition of being “cold-blooded,” she is effectively providing an electric blanket for her eggs.

Pythons are not the only good mothers in the serpentine world. The female King Cobra uses her body coils to draw together large piles of dead vegetation into a nest. She then lays her eggs in the center and settles down to guard her nest against any threat, even elephants.

When the time comes to hatch, two to three months later, the hatchling snake will escape from its egg by making a series of slits in the parchment-like shell using an egg-tooth on the front of its upper lip. The hatchling may exit the shell immediately, or it may rest awhile to absorb the remainder of the yolk sac before venturing out into the world.

VIVIPARITY

Females of viviparous species do not lay eggs, but instead they retain the embryos within their oviducts as they develop, where they receive nutrition from the female across fetal membranes or a placenta, the female only giving birth when her offspring are fully developed and capable of survival. Among the extant reptiles, only the Squamata (snakes and lizards) exhibit “viviparity” (live-birth), but it has evolved independently at least a hundred times within the order. Of the 42 snake families, 11 are entirely viviparous (see Table opposite).

Viviparity is a risky and potentially costly strategy. A female full of offspring may not have the body space available for prey so she may not feed, and if she is killed her entire reproductive investment, and that of her mate, is lost. But viviparity also has advantages. As already mentioned, the oviparous Western Grass Snake does not occur further north than southern Scotland, but the viviparous Northern Adder occurs right up to the Highlands and also on some of the islands off the west coast of Scotland and north of the Arctic Circle in Scandinavia. The female is effectively a mobile incubator. If the weather is inclement she does not venture out, and when she does she can bask and move around as the best basking sites change with the position of the sun. Viviparity is, therefore, the best strategy for snakes living in cold environments. The Northern Adder, the northernmost snake in the world, the Patagonian Lancehead (*Bothrops ammodytoides*), the southernmost snake in the world, and all three species present on Tasmania, are all viviparous, as are many montane species.

It is also an advantage for aquatic snakes to be viviparous. With the exception of a few specialized freshwater turtles, reptile eggs that become

inundated by water will drown. The sea kraits (*Laticauda* spp.) are marine snakes with flattened paddle-shaped tails, but they are oviparous and must come onto land to lay their eggs, and this requirement means they cannot venture far out into the ocean compared with the true seasnakes (*Hydrophis* spp. and its allies), which are viviparous and not tied to coastlines or islands. The most widely distributed naturally occurring snake in the world, the Pelagic Seasnake (*Hydrophis platurus*) may live its entire life out of sight of land, simply birthing its neonates directly into the ocean.

Neonates are born contained within a membranous sac from which they quickly escape and become independent. Although the offspring of some species, including many vipers, remain with the female parent for a short time, and may achieve some protection that way, they are independent and must find prey and ultimately survive on their own.



REPRODUCTIVE STRATEGIES OF SNAKES

SUPERFAMILIES	FAMILY	SUBFAMILY	SUPERFAMILIES	FAMILY	SUBFAMILY
	Anomalepididae		Xenodermoidea	Xenodermidae	
	Leptotyphlopidae	Epictinae	Pareoidea	Pareidae	Pareinae
		Leptotyphlopinae			Xylophiinae
Typhlopoidea	Gerrhopilidae		Homalopsoidea	Homalopsidae	
	Typhlopidae	Afrotyphlopinae	Viperoidea	Viperidae	Azemiophinae
		Asiatyphlopinae			Crotalinae
		Madatyphlopinae			Viperinae
		Typhlopinae			
Xenotyphlopidae		Colubroidea	Colubridae	Chrysopeleinae Colubrinae	
Anilioidea	Aniliidae			Calamariidae	
	Tropidophiidae			Grayiidae	
Uropeltoidea	Anomochilidae			Dipsadidae	Carphophiinae
	Cylindrophiidae				Dipsadinae
	Uropeltidae				Xenodontinae
<i>incertae sedis</i>	Bolyeriidae			Natricidae	
<i>incertae sedis</i>	Xenophidiidae			Sibynophiidae	
Pythonoidea	Loxocemidae			Pseudoxenodontidae	
	Pythonidae				
	Xenopeltidae				
Booidea	Boidae		Elapoidea	Atractaspidae	Aparallactinae Atractaspinae
	Calabariidae			Cyclocoridae	
	Candoiidae			Lamprophiidae	
	Charinidae			Psammophiidae	
	Ungaliophiidae			Prosymnidae	
	Erycidae			Pseudaspidae	
	Sanziniidae			Pseudoxyrhopiidae	
				Elapidae	Elapinae
Acrochordoidea	Acrochordidae				Hydrophiinae

- All genera and species oviparous (lay eggs)
- All genera and species viviparous (bear live young)
- Both oviparous and viviparous genera and species

LEFT | A neonate Copperhead (*Agkistrodon contortrix*) is born in a membraneous sac that ruptures soon after it escapes and takes its first breath.



COLOR CHANGE

Some snakes have young that are differently patterned than the adults. Juvenile emerald treeboas (*Corallus batesii* and *C. caninus*) and green tree pythons (*Morelia azurea* and *M. viridis*) have neonates and hatchlings respectively that are orange or yellow but which become green between 18 and 24 months. This is known as an ontogenetic color change.

PARTHENOGENESIS

Parthenogenesis is the scientific term for virgin birth. It occurs when a female lays fertile eggs, or gives birth to neonates, without ever having mated with a male. There are two kinds of parthenogenesis. Facultative parthenogenesis is when a female of a usually sexual species produces

LEFT & ABOVE | Some snakes have young that are differently patterned than the adults. Juvenile Southern Green Tree Pythons (*Morelia viridis*) have hatchlings that are orange or yellow, but which become green between 18 and 24 months. This is known as an ontogenetic color change.

RIGHT | A dicephalic Cornsnake (*Pantherophis guttatus*), most such snakes die young but some survive to adulthood.



offspring or eggs without contact with a mate; it might be seen as a sort of last resort in order to reproduce, and it has been recorded in boas and anacondas, pythons, filesnakes, gartersnakes, and rattlesnakes. The offspring from parthenogenetic events in boas and pythons are all female, whereas those in the filesnakes and other more advanced species are all males.

The other form of parthenogenesis is obligate parthenogenesis; these species always reproduce parthenogenetically and exist as an all-female species. There are numerous obligate parthenogenetic species among the lizards across at least seven families, but there is only one obligate parthenogenetic snake species known, the Brahminy Blindsnake, or “flowerpot snake” (*Indotyphlops braminus*). Being able to produce

offspring without the need to find a mate makes this tiny snake a super-colonizer, and has enabled it to establish beachheads worldwide, traveling in the root-balls of horticultural or crop plants.

DICEPHALISM

A snake should only possess a single head, but on occasion infant snakes are born or hatch which are dicephalic: they possess two heads at the same end of the same body. Usually these snakes do not survive long, due to other more fatal abnormalities, but sometimes they do survive and can grow to adulthood in captivity, though they are less likely to survive in nature.

DIET

While there are lizards that occasionally, or habitually, eat vegetation, the snakes are completely carnivorous and hunt and devour a diverse range of prey species, from ants to antelope. Many snakes are euryphagous (generalist feeders), taking prey from a range of different taxonomic groups and of varying sizes, whereas others are stenophagous (specialized feeders) with very specific diets. Snakes are highly adapted predators that use their sense organs to good effect when hunting and killing prey. While some lizards, such as monitor lizards (Varanidae), are noted scavengers, whether snakes will eat carrion is a much-discussed topic. For instance, a rattlesnake seen eating a road-killed rodent could simply be following up on a prey animal it had envenomed earlier, and which had become disorientated, run

onto the road, and been hit by a vehicle. A recent video of a whipsnake (*Demansia* spp.) eating grapes more likely showed a snake tracking a rodent and mistakenly eating the fruit the rodent had left its scent on, perhaps by urinating on it.

HOW SNAKES KILL PREY

Many snakes feed on prey that really does not fight back in any significant way. Eggs; invertebrates, like termite larvae, earthworms, and slugs, or even vertebrates such as frogs, can be consumed without the need to dispatch them first because they are unlikely to cause any damage during the swallowing process. The slime of slugs, snails, and earthworms is seemingly neutralized by oral secretions produced by specialized molluskophagous or vermivorous snakes. It seems brutal but a Western Grass Snake



RIGHT | Southern African Python (*Python natalensis*) waits while the constriction process kills its prey, after which it will swallow the prey head first.

LEFT | The Eastern Hognose Snake (*Heterodon platirhinos*) feeds on toads. When toads feel threatened they will inflate their bodies, but the enlarged rear teeth of the hognose snake will deflate the toad and oral secretions may reduce its struggles.



(*Natrix helvetica*) has no problem swallowing a frog alive. Some toads inflate themselves as a defense and species like the hognose snakes (*Heterodon* spp.) quickly deflate them again using enlarged teeth positioned in the rear of the mouth.

But not all prey is easy or safe to swallow alive, and snakes have evolved two systems to help them deal with more hazardous meals. The first is constriction, whereby the snake wraps its coils around the prey animal and tightens its grip until the prey is dead. Although bones may be broken in the process, crushing the prey to death is not the purpose of constriction—nor does the snake kill its prey by suffocation, preventing its lungs from obtaining air, as previously believed. Death through constriction is extremely rapid because the constricting coils are so powerful that they literally stop the flow of blood around the prey's

body, preventing oxygen from reaching the brain and other organs, leading to unconsciousness in seconds, and death through cardiac arrest soon afterward. A version of constriction without the coiling is also used by snakes that hunt underground, such as the Eastern Indigo Snake (*Drymarchon couperi*). Entering a rodent burrow, it will react instantly to any prey contact so that it could easily be swallowing one rat while simultaneously pinioning and killing several others against the burrow walls, floor, and ceiling.

The other method of killing prey is, of course, venom, but the delivery mechanism varies greatly from rear-fanged snakes to the front-fanged elapids and vipers (see Snake Dentition and Fangs, pp.16–17), and when does a mildly toxic oral secretion become a venom? There are venoms that cause paralysis, specifically of the

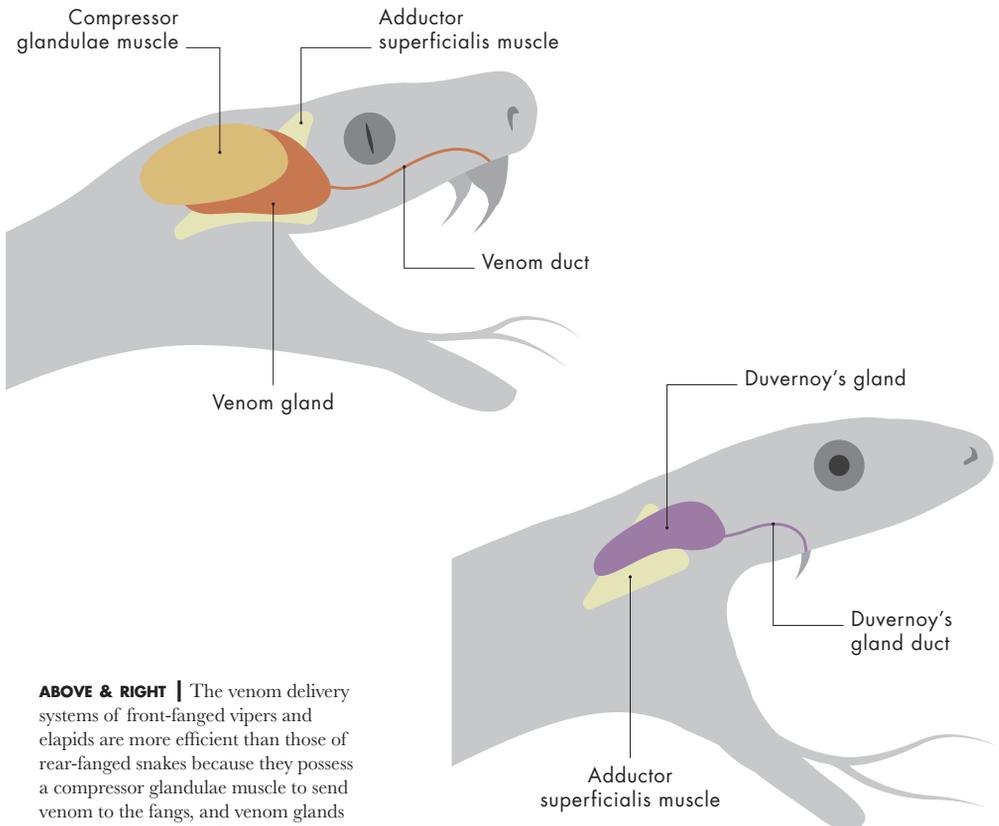
respiratory or neuromuscular system (pre- and post-synaptic neurotoxins, myotoxins); venoms that affect the blood and its circulation (pro- and anticoagulants, haemorrhagins, haemolycins, and platelet inhibitors); and venoms that attack tissues (cytotoxins), muscles (myotoxins again), or specifically the heart (carditoxins, sarafotoxins) or kidneys (nephrotoxins).

Any particular snake venom may contain a cocktail of several of these toxin types and be finely tuned by the predator-prey arms race to deal with specific prey. A widely distributed snake species, which feeds on different prey in different countries or habitats, may exhibit significantly

different prey-specific venom compositions across its range. Venom composition may also change ontogenetically within a single individual as it matures from a juvenile feeding on lizards to a more mammalian diet as an adult.

In contrast to most lizards, snakes swallow large prey whole so, for those species that prey on animals broader than their own head, the evolution of articulatable lower jaws that are not fused at the chin and spare skin in the mental groove down the center of the snake's throat are essential evolutionary adaptations. Most advanced snakes feed on relatively large prey and they are known as "macrostomatans" (big mouths).

VENOM DELIVERY



ABOVE & RIGHT | The venom delivery systems of front-fanged vipers and elapids are more efficient than those of rear-fanged snakes because they possess a compressor glandulae muscle to send venom to the fangs, and venom glands can store a reservoir of venom while rear-fanged Duvernoy's glands do not.



LEFT | Dunn's Groundsnake (*Atractus dunnii*) is one of legions of snakes worldwide that feed almost exclusively on earthworms and which often possess oral glands that neutralize the worm's slimy secretions.

INVERTEBRATE PREDATORS

A large number of snake species feed on invertebrates as juveniles, but graduate to vertebrate prey as they reach maturity. What we are concerned with here are those snakes that continue to prey on invertebrates, either totally or primarily, throughout their lives. The five families of fossorial scolecophidian blindsnakes and threadsnakes eat termite and ant eggs and larvae, entering the nests of sometimes aggressive ant species with impunity as they have smeared their close-fitting and sting-proof scales with a secretion that deters attack. These small snakes just seem to absorb eggs or larvae into their tiny mouths.

Next are the “goo-eaters,” snakes that specialize in feeding on slugs and snails, the genera *Sibon*, *Dipsas*, and *Tropidodipsas* in the Americas, *Duberria* in Africa, and *Pareas*, *Aplopeltura*, and *Asthenodipsas* in Asia. Some of these specialist feeders possess oral glands that produce a secretion, which not only neutralizes the slimy mucus of the mollusk but also immobilizes it and facilitates its extraction from the shell, when the snake inserts one half of its lower jaw, snags the snail with its teeth, and pulls. Earthworms are common prey for many snakes that demonstrate generally catholic diets, but they

are the sole or primary prey of the shieldtails and earthsnakes (Uropeltidae), the spine-jawed snakes (Xenophidiidae), and snakes from several other families, including the Indian worm-eating snakes (*Trachischium* spp.), Sri Lankan roughsides (*Aspidura* spp.), North American wormsnakes (*Carphophis* spp.), and the Papuan stout-tailed snakes (*Calamophis* spp.). Even front-fanged venomous snakes, such as the elapids the Fiji Snake (*Ogmodon vitianus*) and the Papuan worm-eating snakes (*Toxicocalamus*), and the Uzungwe Worm-eating Viper (*Atheris barbouri*) feed on earthworms, while Hemprich's Coralsnake (*Micrurus hemprichii*) shows a preference for velvet worms (Onychophora).

There are also snakes that specialize in eating much less innocuous invertebrate prey, such as the Queen Snake (*Regina septemvittata*), which eats crayfish; the White-bellied Mangrove Snake (*Fordonia leucobalia*), which eats freshly sloughed crabs and mud lobsters; the Central American Black-ringed Centipede Snake (*Scolecophis atrocinctus*); and African centipede-eaters (*Aparallactus* spp.) and some populations of saw-scaled or carpet vipers (*Echis* spp.), which possess venom specifically to deal with the highly venomous scorpions they hunt.



LEFT | Natural pest control—a Northern Watersnake (*Nerodia sipedon*) swallowing a male Round Goby (*Neogobius melanostomus*), which is a black color in the breeding season. This goby is an aggressive invasive in Lake Michigan.

RIGHT | A juvenile Copperhead (*Agkistrodon contortrix*) attracts its prey within strike range by waving its yellow tail, a behavior known as caudal luring.

VERTEBRATE PREDATORS

Fish, ranging from gobies to catfish and eels, are the primary prey for the seasnakes and sea kraits (marine Hydrophiinae), the aquatic mudsnakes (Homalopsidae), the curious Tentacled Snake (*Erpeton tentaculatum*), the filesnakes (Acrochordidae), some of the watersnakes (Natricidae), African watersnakes (Grayiidae), the Annulated Water Cobra (*Naja annulata*) in Central Africa, the Aquatic Coralsnake (*Micrurus surinamensis*) in the Amazon, and the Eastern Cottonmouth (*Agkistrodon piscivorus*) in the USA. On Rennell Island in the Solomon Islands, the two sea kraits present partition the available resources: the endemic Lake Te-Neggano Sea Krait (*Laticauda crockeri*) preys on the native Dusky Sleeper, a goby (*Eleotris fusca*), whereas the Colubrine Sea Krait (*L. colubrina*), which enters the lake from the ocean, feeds on the native Pacific shortfinned eel

(*Anguilla obscura*), while neither eats the introduced Mozambique Tilapia (*Oreochromis mossambicus*).

There are even seasnakes that specialize on fish eggs: the turtle-headed seasnakes (*Emydocephalus* spp.) scrape goby eggs off the coral, while the Graceful Seasnake (*Hydrophis gracilis*) inserts its small head into the seabed burrows of gobies and vacuums up the eggs.

Frogs and other anurans are favored prey of snakes at all stages of their development. The cat-eyed snakes (*Leptodeira* spp.) seek out and eat the eggs of treefrogs that have been laid on leaves over ponds, many aquatic snakes will gorge on tadpoles while they are available, and a wide range of snakes will take adult frogs and toads, the Yamakagashi or Tiger Keelback (*Rhabdophis tigrinus*) even sequestering the bufotoxins from its toad prey into its own skin and eggs to make itself and its unborn offspring both venomous and



poisonous. Salamanders and newts are preyed upon by snakes, such as the euryphagous Ringneck Snake (*Diadophis punctatus*), and the more stenophagous Red-bellied Mudsnake (*Farancia abacura*), which specializes on aquatic salamanders known as sirens (Sirenidae) and amphiumas (Amphiumidae). The limbless amphibians known as caecilians (Gymnophiona) fall prey to the South American Pipesnake (*Anilius scytale*) and the Red-tailed Coralsnake (*Micrurus mipartitus*). Some snakes, such as the Death Adders (*Acanthophis* spp.) and the cantils (*Agkistrodon bilineatus* and *A. taylori*) attract their prey by using a caudal lure, a yellow or white tail tip that waves about slowly to tempt frogs within range.

Along with frogs, it would be expected that small lizards form a large part of the diet of numerous tropical and temperate snakes. Certainly, they form the bulk of the diets of many

desert-dwelling snakes such as sand vipers (*Cerastes* spp.) or the Namib Sidewinder (*Bitis peringueyi*), because lizards are more abundant than any other vertebrates in such environments, but a great many terrestrial and arboreal rainforest and temperate snakes are also saurophagous. The Central American Road Guarder (*Coniophanes lineatus*) eats venomous snakes, but it is also sometimes known by the name Lizard-Killer because it also hunts lizards. Worm-lizards (Amphisbaenia) feature strongly in the diets of fossorial and semi-fossorial snakes such as the Painted Coralsnake (*Micrurus corallinus*), while the Desert Coralsnake (*M. tschudii*) and the southern African quill-snakes (*Xenocalamus* spp.) feed exclusively on amphisbaenians.



Nothing fits inside a snake quite so well as another snake (except perhaps for earthworms, eels, amphibia, and caecilians), and there are a great many snakes that occasionally or frequently devour other ophidians, a dietary behavior known as ophiophagy—it is not cannibalism unless they eat their own species, but many species, especially elapids, do that too. Notable snake-eaters include the American kingsnakes (*Lampropeltis* spp.), King Cobra (*Ophiophagus hannah*)—the clue is in the generic name—Asian kraits (*Bungarus* spp.), the African filesnakes (*Gonionotophis*, *Limaformosa*, and *Mehelya* spp.), and the Australian bandy-bandy (*Vermicella* spp.) The Black-headed Python (*Aspidites melanocephalus*) and its relative, the Woma (*A. ramsayi*), are desert pythons that feed on both lizards and snakes, including monitor lizards and elapids, as well as occasional mammals, and the lack of heat-sensitive pits in their labial scales hints at a primarily ectothermic diet.

Crocodiles might seem an unusual prey group for snakes, but there are a number of species that have managed to predate crocodylians. The Green and Yellow Anacondas (*Eunectes murinus* and *E. notaeus*) frequently prey on caimans, while Australian Olive and Water Pythons (*Liasis olivaceus* and *L. fuscus*) are known to take small crocodiles. The most famous cases involve the Burmese Python (*Python bivittatus*), which was accidentally introduced to Florida where they have been known to kill and eat alligators. And not to be left out, there is a case of a Puff Adder (*Bitis arietans*) eating a tortoise.

A number of snakes specialize in eating birds. The Boomslang (*Dispholidus typus*) hunts chameleons but it is also an expert at entering the pendulous nests of weaver birds (Ploceidae) in order to eat their chicks. The tropical American Puffing Snake (*Phrynonax poecilonotus*) is another arboreal raider of bird's nests and will endure mobbing by the parent birds in order to steal from



OPPOSITE | Misquito Coast Coralsnake (*Micrurus mosquitenis*) preying on a Red Coffeesnake (*Ninia sebae*).

LEFT | A Boomslang (*Dispholidus typus*) eating a helmetshrike (*Prionops* sp.) chick.

BELOW | A Southern African Python (*Python natalensis*) may spend hours swallowing an antelope but it will not choke because it can extend its glottis (airway) out of the front of its mouth as a muscular breathing tube.

their nests. On Chappell Island, off Tasmania, the Tigersnake (*Notechis scutatus*) enters the subterranean burrows of mutton birds to gorge on their chicks over a 6–8 week period, before fasting until the next breeding season, ten months away. Then there is the Brown Treesnake (*Boiga irregularis*) on Guam (see Feral and Invasive species, p.63).

And, finally, mammals. It could well have been the explosion in early small mammal diversity 65 MYA that triggered the radiation of the snakes, and today there are a huge number of ratsnakes, housesnakes, rattlesnakes, and other serpents for which a warm, furry endotherm is the ideal meal. Mice and rats breed in large numbers and snakes are the most natural predators of their legions. Bats too have their predators, in the heat-sensitive Amazonian Treeboa (*Corallus hortulanus*) positioned in ambush on a night-blooming *Parkia* plant, awaiting a nectar-feeding bat, or the pastel-colored Cave Racer (*Elaphe taeniura ridleyi*) hunting around bat roosts in the Batu Caves of peninsular Malaysia.



The African rock pythons (*Python sebae* and *P. natalensis*) and the Reticulated Python (*Malayopython reticulatus*) are giant snakes quite capable of killing and swallowing large prey, including antelope, pigs, even an adult female sun bear in the case of the latter species, and it is also these three species that have, on rare occasions, accomplished the unthinkable: they have ambushed, killed, and swallowed human beings whole.

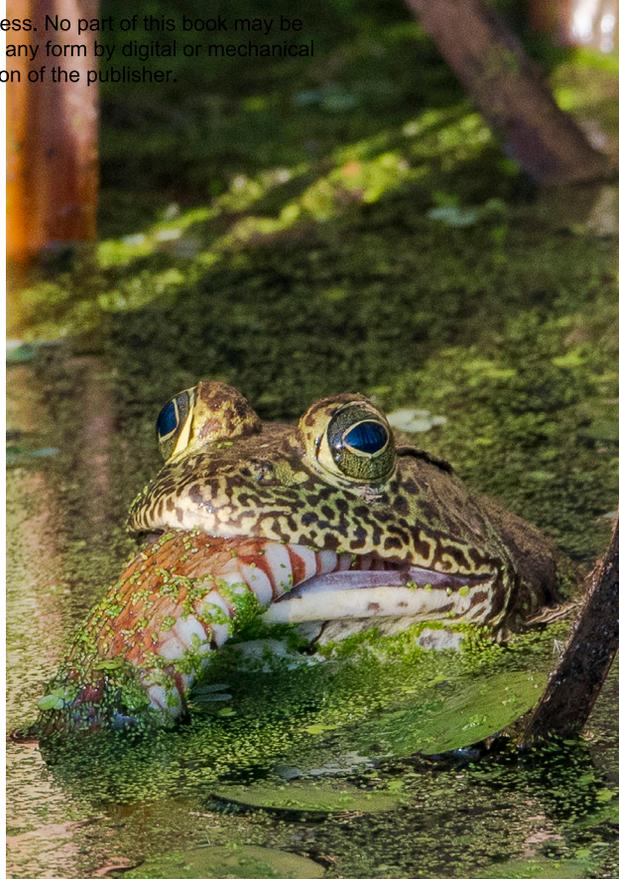
DEFENSE

As will be seen, snakes have many enemies, and they have evolved some ingenious ways of avoiding being eaten, some of which involve real threats, but others that are more smoke and mirrors and trickery. While some snakes announce their presence, others are truly adept at hiding in plain sight.

PREDATORS AND ENEMIES OF SNAKES

Snakes may fall prey to venomous invertebrates like centipedes, spiders, scorpions, or hosts of smaller insects like army ants or yellow crazy ants, but their primary predators are among the vertebrates. Large voracious amphibians such as the Cane Toad (*Rhinella marina*) or African Bullfrog (*Pyxicephalus adspersus*) will eat snakes. The Tiger Shark (*Galeocerdo cuvier*) is one of the few fish that can eat highly venomous seasnakes with impunity. Snapping Turtles (*Chelydra serpentina*), monitor lizards (*Varanus* spp.), and tegus (*Tupinambis* spp.) can all make short work of small to medium-sized snakes, and, of course, crocodylians will also opportunistically eat snakes caught swimming. As discussed earlier, snakes may also be eaten by other snakes.

Many birds will eat snakes, from the Common Buzzard (*Buteo buteo*) to fish eagles (*Haliaeetus* spp.), the Serpent Eagle (*Spilornis cheela*), the Secretary Bird (*Sagittarius serpentarius*), and the kookaburras (*Dacelo* spp.). Among the mammals are the obvious culprits, mongooses and meerkats (Herpestidae), but also some surprises such as the European Hedgehog (*Erinaceus europaeus*); however, the biggest snake killer has to be the upright ape known as *Homo sapiens*. The reaction of many humans upon sighting a snake is to reach for the nearest heavy



implement to kill it, regardless of whether the snake is dangerous or represents any kind of threat. Sometimes snakes are persecuted in huge numbers, such as in the “rattlesnake roundups” that are still permitted in some US states today. But humans also kill snakes accidentally. A stretch of warm, wet black-top might seem a great place to bask to a snake on the prowl, but increased road

ABOVE | An American Bullfrog (*Lithobates catesbeiana*) attempting to swallow a live Florida Banded Watersnake (*Nerodia fasciata pictiventris*) tail-first, in Florida’s most polluted lake, Lake Apopka.

RIGHT | The East African Gaboon Viper (*Bitis gabonica*) has a geometric pattern of pastel colors and a head like a dead leaf that helps it blend in on the forest or woodland floor.

building and traffic has led to rapid and clearly discernible declines in snake populations along those roads. Although snakes have no defenses against automobiles, they do have a wide range of defenses that they can use against other flesh and blood enemies.

CAMOUFLAGE AND CRYPISIS

Camouflage is the art of concealing oneself from potential enemies, by adopting the color, shape, or behavior of other objects in the environment and thereby blending into the background.

Crypsis is a somewhat broader term that includes mimicry, pretending to be a different and more dangerous animal, and altering one's activity cycle to avoid predation.

Many snakes are sit-and-wait ambushers, remaining motionless for hours, or days, for prey to come within strike range. For them, camouflage is useful both for avoiding giving

their presence away to their prey, and for evading detection by an enemy. A giant East African Gaboon Viper (*Bitis gabonica*) lies invisible in the forest leaf litter, its Persian carpet body pattern of pastel geometric designs and its large leaf-shaped head, complete with dark midvein, breaking up its outline so effectively that it is difficult to see even when you know it is there, somewhere, its only movements being its slow respiration, and the occasional flicker of its vertically elliptical pupils; the only movement, that is, until it strikes! This huge viper, 5 ft (1.5 m) long, weighing 44 lb (20 kg), fatter than a human arm, hiding 2-inch-long (5 cm) fangs inside a head almost as large as a human hand, is lying there in plain sight, yet it is virtually invisible. This is camouflage in its most effective and visceral form.



APOSEMATISM AND MIMICRY

While the Gaboon Viper is effectively saying “move along, nothing to see here,” the American coralsnakes (*Micrurus* spp.) are gaudily sending out a different message, one of “look at me, I’m patterned with warning colors so you’d better give me a wide berth”; at least, that is one interpretation of the vivid red, yellow, and black bands of these highly venomous snakes. Another possibility could be that when the semi-fossorial coralsnake is uncovered in the leaf litter, or exposed by the rolling of a log, its rapid movements and the swirling of its contrastingly colored coils may serve to confuse the uncoverer just long enough for the coralsnake to make its escape. That said, these three colors are used as warning colors by a wide variety of venomous or poisonous animals, and the bite from a coralsnake is an extremely serious accident so, perhaps, it is a bit of both: warn and confuse.

Color-change is a useful defense and, while snakes are not chameleons, they can sometimes exhibit flashes of colors not normally on display, such as the black of the inside of the gaping mouth of a usually gun-metal or brown Black Mamba (*Dendroaspis polylepis*), the sudden flash of brilliant white in the mouth of the aptly named Cottonmouth (*Agkistrodon piscivorus*), or the inflation of the throat, exposing interstitial skin of a contrasting color to the scales in the Boomslang (*Dispholidus typus*). These are all aposematic warnings best heeded.

If possessing a particular color pattern is a good way to avoid unwanted attention from potential predators, then copying those patterns should also bring an element of protection to a harmless species. This is where mimicry comes in, and a classic example would be the harmless Scarlet Kingsnake (*Lampropeltis elapsoides*) of southeastern USA, which mimics the pattern



of the venomous Eastern Coralsnake (*M. fulvius*) from the same geographical location. The order of the bands is important here and the famous rhyme “Red to yellow, kill a fellow; Red to black, venom lack” easily distinguishes between the two. But in Latin America there are coralsnakes with “red to black” coloration, and also mildly venomous species such as the False Coralsnake (*Erythrolamprus aesculapii*) to further confuse the situation. It is now believed mimicry is not as straightforward as it would initially seem to be.

LEFT | A gaping Black Mamba (*Dendroaspis polylepis*) shows off the contrastingly dark interior of its deadly mouth as a threat.

BOTTOM & RIGHT | A venomous Eastern Coralsnake (*Micrurus fulvius*), bottom, with the warning colors arranged as “red to yellow, kill a fellow.” The harmless mimic, the Scarlet Kingsnake (*Lampropeltis elapsoides*), right, displaying “red to black, venom lack.”



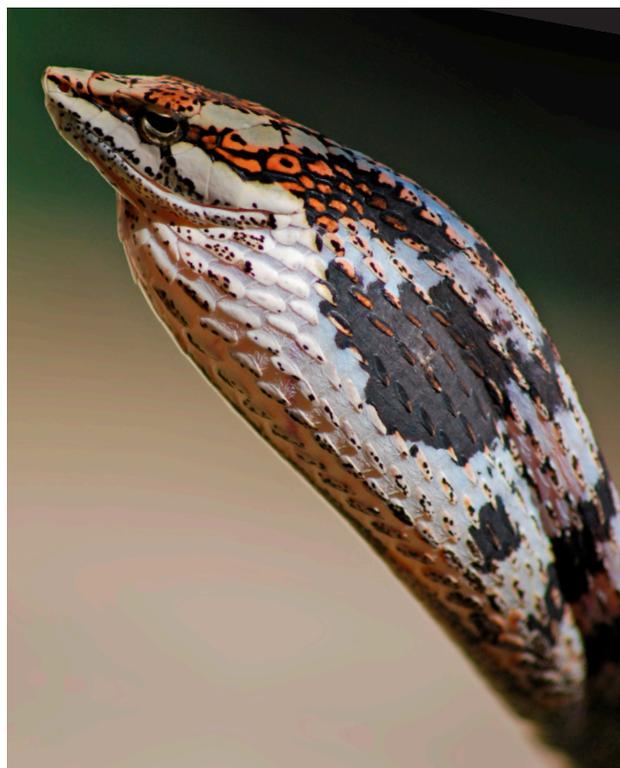
VISUAL WARNING DISPLAYS

It has already been mentioned that a Boomslang may inflate its throat as a warning to potential enemies, and it is not alone: this is also practiced by African twigsnakes (*Thelotornis* spp.), neotropical puffing snakes (*Phrynonax* spp.), and the Tiger Ratsnake (*Spilotes pullatus*). But there is one very famous visual defensive display: the hooding of the cobra (*Naja* spp.). It is only possible for the cobra to adopt its instantly recognizable posture because of something we established in the discussion about the snake's skeleton: snakes have no sternum (breastbone) so the ends of the ribs distal to the backbone are free and capable of being spread into the hood shape by the intercostal muscles between them. This is emphasized by the cobra rising from the ground to further intimidate its enemy and, if necessary, making short mock rushes forward, or hissing its annoyance.

Hooding is not confined to the cobras: it has also evolved in the King Cobra (*Ophiophagus hannah*) and the Asian mock cobras (*Pseudoxenodon* and *Plagiopholis* spp.), the African coral snake (*Aspidelaps lubricus*), Australian blacksnakes (*Pseudechis* spp.), and the South American False Water Cobra (*Hydrodynastes gigas*), so clearly the sight of a snake raising up to a third of its body off the ground and spreading a hood is internationally viewed as a threat posture. Such an effective warning is the cobra's hood that it is believed that Slow Lorises (*Nycticebus* spp.) mimic them by raising their arms over their head to make the shape of the hood, their own large eyes recreating the markings of the cobra.

AUDIBLE WARNING DISPLAYS

Obviously, the most basic audible warning a snake can issue is a long drawn-out hiss, especially the loud, long, intimidating hisses of the Russell's



vipers (*Daboia russelii* and *D. siamensis*) or the Puff Adder (*Bitis arietans*), or even that of Bull Snake (*Pituophis catenifer*). Common cobras in Asia seem to have two different hisses: a short “I’m irritated” *tst-tst-tst*, and the more threatening, more drawn out “Now I’m serious” hiss. Large King Cobras are said to utter a deep growl as a warning. But hissing is a costly business. Every time a snake hisses it expels a breath of air, and with that air, moisture. That does not matter in a humid rainforest, but in a particularly arid habitat like desert it might be better to find an alternative and less water-costly means of making a sound.

The Copperhead (*Agkistrodon contortrix*) of eastern North America will warn off intruders by vibrating its tail on dead leaves in its woodland home. In the absence of dead leaves, the rattle of a rattlesnake (*Crotalus* spp.) is a marvelous adaptation and the reason they are often called

“buzztails.” A neonate rattlesnake bears a tiny button on the end of its tiny tail, and although it may rattle its tail, at this point it makes no sound. But every time the snake sheds its skin it adds a link to the proximal end of its rattle until, over time, it grows a multi-linked rattle that will produce an audible and instantly recognizable sound when shaken rapidly by specialized muscles in its tail. To debunk a myth, you cannot age a rattlesnake by the number of links because they are added at irregular intervals as it grows, and long rattles are fragile and prone to breaking.



FAR LEFT | The Indian Cobra (*Naja naja*) is one of the most instantly recognizable snakes because of its spectacle-marked hood.

LEFT | The first stage in the threat of a twigsnake (*Thelotornis* spp.) is to inflate its neck, the next is to flatten its head like a lance. There is no antivenom for its bite should these postures be ignored.

RIGHT | This Tiger Rattlesnake (*Crotalus tigris*) has a nine-link rattle with which it will produce that familiar warning sound. Composed of dry skin, with a link added every time the snake sloughs, there is nothing inside the rattle (inset), each link fits loosely into the two previous links so that any movement of the tail will cause them to rattle together.





Rattlesnakes are endemic to the Americas so there are none in Asia or Africa, but there are snakes there that issue a similar warning sound, the carpet or saw-scale vipers (*Echis* spp.). These small but highly venomous snakes exhibit an unusual arrangement of the dorsal scale rows along their flanks: they are arranged more obliquely than the scales on the dorsum of the back, and each of the scale keels is finely serrated. When the saw-scale viper feels threatened it will form its body into a series of concentric curves, while maintaining its head to the front. It will then begin to move backward, away from the threat; but, as its coils move against one another the serrated scales make a rasping, sawing sound, aptly warning that to approach within the range of the little viper's jabbing strike would be a foolish move, even for a large predator.

Perhaps the strangest sound-making is that of the Sonoran Coralsnake (*Micruroides euryxanthus*), which engages in cloacal-popping, expelling air from its cloaca; though how effective a warning it is must be open to question.

LEFT | Saw-scale and Carpet Vipers (*Echis* spp.) have specially arranged serrated rows of scales on their flanks so that when they rub their concentric body coils together they make a sawing sound.

ABOVE | The Sonoran or Arizona Coralsnake (*Micruroides euryxanthus*) has warning colors, but it also raises its tail and makes a popping sound with its cloaca.

RIGHT | A Mozambique Spitting Cobra (*Naja mossambica*) sending a cloud of venom toward a perceived enemy.

FAR RIGHT | This Iberian Grass Snake (*Natrix astreptophora*) is playing dead, a behavior known as thanatosis.



OTHER TACTICS

There are many fast-moving diurnal snakes that earn the names “whipsnake” (*Masticophis* in North America, *Demansia* in Australia) or “racer” (*Coluber* in North America, *Platyceps* in Eurasia), and all these species, and more, put their speed to good use when fleeing a potential predator. Other snakes adopt the exact opposite tactic: they stay where they are and play dead, a behavior known as thanatosis, rolling on their backs with their tongues lolling out, presumably only a successful technique if the threat is not a scavenger that eats carrion. The Ringhals Spitting Cobra (*Hemachatus haemachatus*), American hognose snakes (*Heterodon* spp.), and the grass snakes (*Natrix* spp.) are all well known for this behavior.

Among a disparate array of defenses, perhaps one exemplifies the notion that attack is the best form of defense. The spitting cobras (*Naja* spp.) possess specially adapted fangs that enable them to send twin jets of venom into the face of their perceived aggressor. While the venom of non-spitting cobras is primarily neurotoxic in

composition, that of the spitters is more cytotoxic, breaking down the tissues. When it lands in the eyes of an animal it will start to digest the corneas, causing pain and blindness, and providing the cobra with sufficient time to escape. Many spitting cobras do not even bother with Plan A, raising a hood, going straight to Plan B, spitting when they are only slightly raised off the ground. The venom can be washed from the eyes fairly easily by prolonged bathing with water, but the victim needs to be human to know that. Once they have immobilized their enemy they will effect a rapid escape rather than coming in close for the *coup de grâce*. Interestingly, spitting cobras do not seem to spit when hunting.

CONSERVATION

Many people do not like snakes. That is an unfortunate global reality. But whether their feelings are based on the fear of snakebite, a rational and very real danger for millions of people in the tropics, or on a more irrational revulsion, born out of one of the many myths about snakes, that they are slimy to the touch, for instance, there is no getting away from the fact that snakes have a public relations problem. But whether snakes are actively persecuted, or are threatened by the same factors that impact other wildlife, such as habitat loss, road building, climate change, or pollution, they are still in need of protection, of conservation.

Three billion people, half the world's population, rely on the rice crop to survive. But rice crops also attract legions of rodents which are responsible for losses of 5–10 percent of the rice, with increases in some areas to 20 percent, 30 percent, even 50 percent. These same rodents pass on diseases such as Weil's disease through their

urine, and Lyme disease from the bites of ticks living on the rodents. Snakes are the number one most effective rodent exterminator and they should be encouraged, not discouraged or killed, when encountered living in rice-paddies or plantations of other crops.

RATTLESNAKE ROUNDUPS

In some tropical countries, snakes are also harvested in unsustainable numbers for their skins, meat, and their gall bladders, this last for an unproven tonic for a failing libido. But they are also severely threatened by western practices.

Rattlesnake roundups were started in some US states to remove snakes that were considered a threat to cattle, but over time they have turned into multimillion-dollar entertainment, with thousands of rattlesnakes being collected annually, even shipped in from out of state to keep up with demand. At one time the snakes were slaughtered during or after the events,



ABOVE | Rattlesnakes at the world's largest roundup at Sweetwater, Texas. This is not the best way to educate this young lad to appreciate nature.

LEFT | The Brown Treesnake (*Boiga irregularis*) is at equilibrium within its native range but on Guam it has caused an ecological catastrophe.



but today some (but not all) organizers claim they release snakes back into the wild, and that the roundups are intended to be educational. But rattlesnakes are now thought to grow up knowing their own neighborhoods, and just dumping them into the wild somewhere else, often stressed and in poor condition, does not bode well for their orientation and survival. And with the burgeoning problem of Snake Fungal Disease (SFD) in native US snake populations, the holding together and subsequent release of thousands of stressed snakes back into nature is akin to a super-spreader event, introducing the fungal pathogen to wild populations where it may not have formerly been present.

FERAL AND INVASIVE SPECIES

When this subject was covered in *Lizards of the World*, the emphasis was on the damaging effect that introduced mammals, such as cats, rats, goats, and pigs had on the native lizard faunas, especially those on remote islands. Island snake faunas are also threatened by domestic or invasive animals. For instance, the remotest terrestrial elapid snake in the world, *Ogmodon vitianus*, locally known as *gata ni balabala* (snake

of the mountain ferns), but referred to more widely as the Fiji Snake, is a snake on the brink. This tiny ($< 12\frac{1}{2}$ in/320 mm), semi-fossorial snake is only found on the southern side of Viti Levu, Fiji's main island, 1,200 miles (2,000 km) from its next nearest terrestrial elapid relative, in the Solomon Islands. Close to the evolutionary origins of Australasian elapids, but considered harmless, *Ogmodon* is threatened by the activities of semi-feral village pigs, which root in the soil and will quickly devour any snake uncovered. This unique snake is now listed as Endangered by the International Union for Conservation of Nature (IUCN). If that circumstance seems remote, then consider a recent survey of southern Belgian populations of the Northern Adder (*Vipera berus*) that demonstrated that they are under severe threat from wild boar populations, which are growing rapidly in the absence of predators and the prohibition of hunting. A similar situation may also be occurring with the adder population in the Forest of Dean in the UK, where introduced wild boar have become established and are also protected.

But it is impossible to discuss invasive wildlife and not mention that snakes can be the culprits too. The most famous example was the accidental relocation of the Brown Treesnake (*Boiga irregularis*) from New Guinea to the Pacific island of Guam with returning US military equipment, after World War II. This voracious and highly arboreal predator found itself on an island inhabited by birds that had never encountered snakes before, some of them flightless species, and the treesnake promptly ate seven species to extinction, with three more, including the endemic Guam Rail (*Hypotaenidia owstoni*) being placed into protective custody as the snake populations rose to over a million and scientists struggled to find a way to fight the invasion. On a smaller scale,



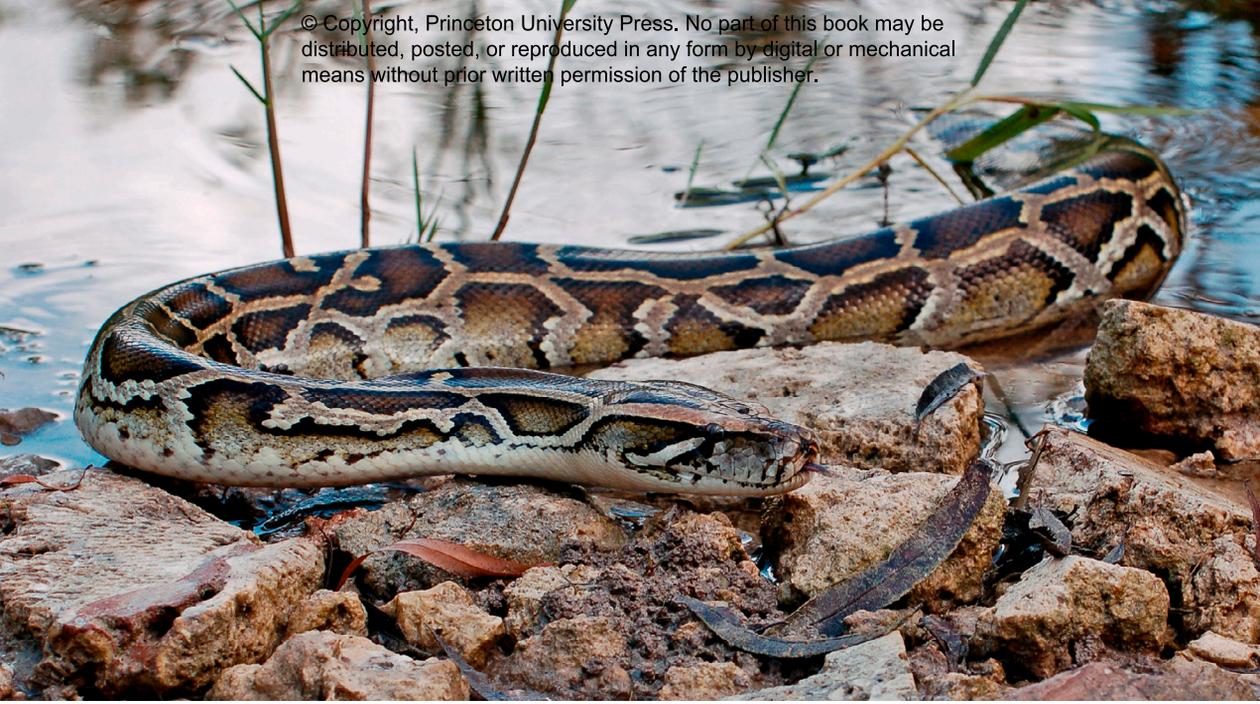
ABOVE | The Antigua Racer (*Alsophis antiguae*) is an example of how a conservation program involving captive breeding can save a species from extinction.

RIGHT | Up to 3,000 Burmese Pythons (*Python bivittatus*) are captured annually in southern Florida.

the Island Wolfsnake (*Lycodon capucinus*) and Common Wolfsnake (*L. aulicus*), both lizard predators, have become established on Pacific and Indian Ocean islands and may have been part of the reason for lizard extinctions and extirpations in countries like Mauritius. On a much larger scale, the release of many juvenile Burmese Pythons (*Python bivittatus*) into southern Florida, whether by a hurricane or by humans, has caused an environmental catastrophe as the pythons grew to over 16 ft (5 m) and began to breed and colonize the sawgrass habitat, not dissimilar to their native Asian riverine grasslands. No longer is the American Alligator (*Alligator mississippiensis*) the unassailable climax predator, because pythons have been found with the remains of alligators in their stomachs. Under greater threat are endangered waterbirds and rare mammals like the already endangered Key Largo Woodrat (*Neotoma floridana smalli*).

SNAKE EXTINCTIONS AND CONSERVATION PROJECTS

Round Island is a tiny (0.65 square miles/1.69 square kilometers) uninhabited islet 14 miles (22.5 km) north of Mauritius, itself an isolated Indian Ocean country. Round Island is home to a number of endemic animals and plants that may once have also inhabited Mauritius. In 1957, recognizing the importance of Round Island, the Mauritian authorities launched a conservation program to protect its fauna and flora, beginning with the eradication of invasive goats and rabbits.



In 1976, the Jersey Wildlife Preservation Trust (JWPT) got involved and set up successful captive breeding programs for the endangered reptile fauna, comprising two skinks, three geckos, and a snake, the Round Island Keel-scaled Boa (*Casarea dussumieri*). But the rescue came too late for the Round Island Burrowing Boa (*Bolyeria multocarinata*), which has not been seen since 1975 and is listed as Extinct by the International Union for the Conservation of Nature (IUCN).

Another rescue project is underway on Christmas Island, an Australian External Territory just south of western Java, which has been used for phosphate mining, currently houses an immigration center for asylum seekers, and was also utilized as a quarantine center for returning Australians in the early days of the Covid-19 crisis. The main threat to the island's fauna was caused by the accidental introduction of the invasive Asian Yellow Crazy Ant (*Anoplolepis gracilipes*), which will kill small vertebrates. Of the four endemic lizards, one is Extinct, two are Extinct in the Wild, and one is Endangered, as is

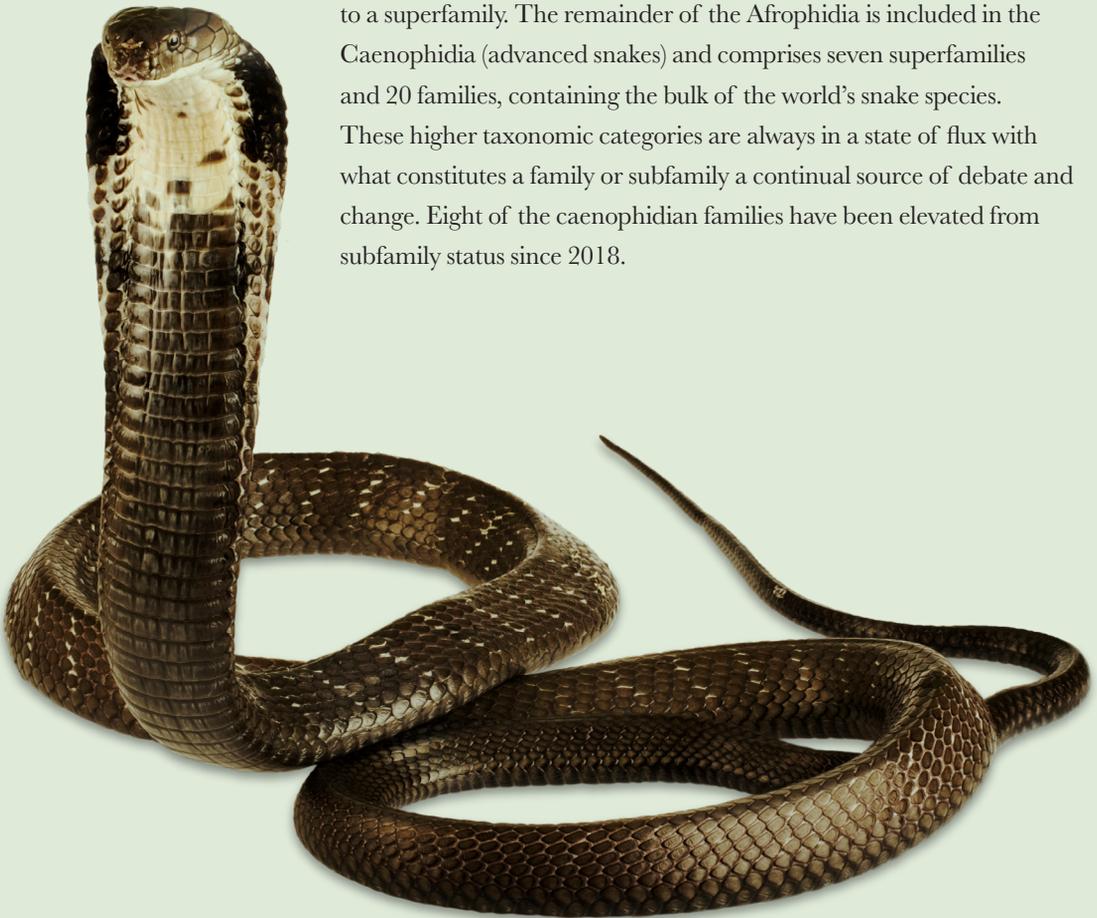
the Christmas Island Blindsnake (*Ramphotyphlops exocoeti*), according to the IUCN.

The Caribbean has witnessed a number of snake extinctions including the Barbados Racer (*Erythrolamprus perfuscus*) and the St. Lucia Cribo (*Clelia errubunda*), but one resounding success is the JWPT captive breeding and reintroduction program for the Antiguan Racer (*Alsophis antigueae*). And other snake species have proven themselves to be "Lazarus species." Cropani's Boa (*Corallus cropanii*) was thought to have gone extinct in the Atlantic coastal forests of Brazil in 1954, but a specimen was found alive and well in 2017 and is now being radiotracked. Similarly the Atlán Long-tailed Rattlesnake (*Crotalus lannomi*) was thought possibly extinct in Mexico as only the type-specimen, collected in 1966, was known, but in 2008 a living specimen was found. Extinction is a negative and it is often hard to prove a negative. The famous quote states: "Absence of evidence is not evidence of absence," so it is hoped that more Lazarus species will be found. Sadly it is too late for the Round Island Burrowing Boa.

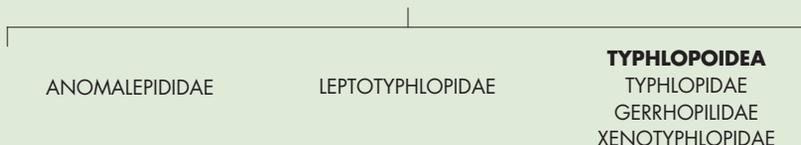
THE SNAKE INFRAORDERS AND SUPERFAMILIES

While there are six lizard infraorders, there are only two for snakes. The Scolecophidia (wormsnakes) contains the five families of blindsnakes and threadsnakes, three of which are placed in a single superfamily, Typhlopoidea. The second infraorder is the Alethinophidia (true snakes) which is itself divided into two clades, the Amerophidia and the Afrophidia, effectively the “not out of America” and “out of Africa” groups depending on their origins. The Amerophidia contains two families that did not spread further than Central and South America, and the Caribbean, while the Afrophidia contains all other known snakes. The basal Afrophidia are the Henophidia (old snakes), containing three superfamilies with 15 families, although two of these families are *incertae sedis* (of unknown placement) and not allocated to a superfamily. The remainder of the Afrophidia is included in the Caenophidia (advanced snakes) and comprises seven superfamilies and 20 families, containing the bulk of the world’s snake species. These higher taxonomic categories are always in a state of flux with what constitutes a family or subfamily a continual source of debate and change. Eight of the caenophidian families have been elevated from subfamily status since 2018.

BELOW | The majestic King Cobra (*Ophiophagus hannah*) is the “King of Snakes,” though strictly it is not actually a cobra.



SCOLECOPHIDIA



ALETHINOPHIDIA





SCOLECOPHIDIA: SUPERFAMILY TYPHLOPOIDEA

The etymology of Scolecophidia is *solec* = worm, *-ophidia* = snake, so named because these small snakes are long, slender, and subterranean. Most are called blindsnakes although they do possess eyes, albeit reduced to photosensitive cells, under translucent head scales, that warn the snake when exposed to the light.

There are five families. The Anomalepididae (early blindsnakes) is Latin American; the Leptotyphlopidae (threadsnakes) inhabit the Americas, Africa, and Western Asia; the Typhlopidae (cosmopolitan blindsnakes) are distributed worldwide; the Gerrhopilidae (glandular blindsnakes) occur from India to the western Pacific; and the Xenotyphlopidae is endemic to Madagascar. The divergence between the Typhlopidae and Leptotyphlopidae occurred in Gondwanaland in the Early Cretaceous (139 MYA). The families Typhlopidae, Gerrhopilidae, and Xenotyphlopidae are closely related in the superfamily Typhlopoidea, which excludes Leptotyphlopidae and Anomalepididae.

The five families contain 40 genera and 463 species, almost 11.7 percent of all living snakes. With a few exceptions, these snakes are little studied due to their secretive nature and small size. One species, *Indotyphlops braminus*, is encountered around the world; because it is an obligate parthenogen, only females exist, and they reproduce without a male. At least 25 lizard species across seven families utilize this strategy, but only one snake, and its ability to reproduce parthenogenetically has enabled it to colonize much of the world and become the most widely distributed, non-naturally occurring, snake species in the world.

LEFT | The Southern Blindsnake
(*Anilius australis*) from southwestern Australia,
is one of 47 *Anilius* found in Australia.

ANOMALEPIDIDAE

EARLY BLINDSNAKES

OPPOSITE | The Whitenosed Early Blindsnake (*Liotyphlops albirostris*) is named for its white snout, but many anomalepids have white heads.

BELOW | The Trinidad Early Blindsnake (*Typhlophis squamosus*) is also found on mainland South America.



The early blindsnakes or dawn blindsnakes, are included in the endemic neotropical family Anomalepididae, and comprise four genera and 21 species. Believed to be the most basal of all living snakes, anomalepids possess teeth on both the maxillary (upper jaw) and dentary (lower jaw, one to three teeth), unlike typhlopids, gerrhopilids, and xenotyphlopids (teeth only on maxillary bones) and leptotyphlopids (teeth only on dentary bones).

They possess specially adapted skulls for burrowing but lack any vestiges of hind limbs. They also lack a left lung, but possess a tracheal lung, and a functioning left oviduct.

The two centers of anomalepidid radiation are northwest Colombia and southwest Brazil, both of which contain nine species, many of them endemic. The genus *Anomalepis*, the Pacific coastal early blindsnakes, occurs from Colombia to Ecuador and Peru, with the Central American Early Blindsnake (*A. mexicanus*) occurring farther north to Honduras, but not Mexico.



DISTRIBUTION
South America, southern Central America, and Trinidad

GENERA
Anomalepis, *Helminthophis*, *Liotyphlops*, and *Typhlophis*

HABITATS
Lowland rainforest

SIZE
TTL 5¾ in (146 mm) Ecuadorian Dawn Blindsnake (*Anomalepis flavapices*) to 15¾ in (395 mm) Bogota Dawn Blindsnake (*Liotyphlops anops*)

ACTIVITY
Fossorial

REPRODUCTION
Oviparous with clutches of 2–24 eggs

DIET
Ant and termite eggs and larvae, earthworms, caecilians, amphibiaenians

(continued...)

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