

COMPARATIVE COGNITION & BEHAVIOR REVIEWS

Snakes: Slithering from Sensory Physiology to Cognition

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Snakes (*Serpentes*) are scaly, limbless reptiles that share the same taxonomic order (*Squamata*) with lizards (*Sauria*) and amphisbaenians (*Amphisbaenia*). All snakes have an elongated body and are predatory carnivores. This body shape and their feeding modality have a pervasive effect on many aspects of their biology, such as ecology, physiology, and behavior. Snakes inhabit all biogeographic realms except the polar regions and some islands. Within each of these realms they have filled various aquatic, terrestrial, and arboreal niches. In this review, I describe the sensory physiology of snakes and its peculiarities related to their specific way of life. In the final paragraph, I try to summarize the cognitive abilities of snakes and suggest future approaches to further investigate snake cognition and to link it to underlying physiological processes.

Keywords: snakes, physiology, behavior, cognition

Introduction: Snakes Adored, Feared, and Scientifically Neglected

No group of animals induces so many opposing feelings and thoughts as snakes. In cultures of Abrahamic religions, snakes are mainly the animals of evil, endowed with the powers of temptation and falsity, and are responsible for the Fall of Man. In other cultures, they can be symbols and messengers of good or bad. Some snakes can make humans very sick, crippling or even killing them; people of various cultures have been aware of this since the beginning of humanity. Ophidism (the consequences of a venomous snake bite) is an important disease in some parts of the world, causing significant morbidity and mortality (Kasturiratne et al., 2008; Williams et al., 2010). An abnormal fear of snakes, or ophidiophobia, is quite common (Burghardt et al., 2009; Kawai, 2019); so common, in fact, that certain fictional characters have it to enhance the general thrill of movies (Gresh & Weinberg, 2008). Ophidiophobia may have roots in our ancestry. Because an early detection of snakes in the environment can be considered adaptive, Isbell (2006) proposed that snakes might have been a selective pressure for the evolution of

brain and stereoscopic vision in early primates. Evidence shows that pulvinar neurons found in the thalamus of macaques react strongly if pictures of snakes are presented to them (Van Le et al., 2013). Moreover, when infants are shown flickering pictures of various animals on a natural background, their glancing at snakes produces a specific neural response in the occipital region of the brain that has a higher amplitude than that produced by pictures of other animals (Bertels et al., 2020). Because snakes can induce both positive and negative feelings depending on the culture, snakes are the subject of many folktales, myths, and lore (Crump, 2015; Morgan, 2008; Morris & Morris, 1965).

From the standpoint of biology, snakes (Order *Serpentes*) are limbless predatory reptiles with elongated bodies covered with dry, scaly skin. They all have forked tongues and lack eyelids; their eyes are covered with transparent scales (spectacles), which they shed regularly along with the rest of the skin. Together with lizards, snakes make up the order *Squamata* (scaly animals) in the class *Reptilia* (reptiles). There are more than 3,700 species of snakes (Uetz et al., 2022), ranging from the Barbados threadsnake at barely 10 cm long to boas and pythons,

which are more than 5 meter long (Hedges, 2008; Murphy & Henderson, 1997). Snakes are absent from polar regions and some islands but have populated most other ecological niches (Vitt & Caldwell, 2013).

Snakes probably evolved from lizard-like ancestors during the mid- to late Jurassic period, but the quest to find the closest snake ancestor is still ongoing, and no fossils from this period have been found. The oldest snake fossils found to date have hind limbs (Coates & Ruta, 2000). *Najash rionegrina*, a snakelike animal from the Cretaceous period, had a pelvic girdle and protruding, probably functional, hind limbs (Apesteguia & Zaher, 2006). *Najash* was discovered in terrestrial deposits, which suggests that modern snakes have a terrestrial origin. The search for snake origins and ancestry is a vibrant area of research that is, at times, quite contentious. Two hypotheses on snake origins are dominant. The “burrowing lizard hypothesis” is a scenario according to which snakes evolved from burrowing lizards that lost their limbs when they went underground. The competing “marine ancestor hypothesis” states that snakes might have evolved from marine ancestors that lacked limbs. Both hypotheses have ardent proponents and opponents. However, other evolutionary scenarios are possible and are worth considering (Caldwell, 2020). Although fossils are of extreme importance for understanding snake evolution, morphological, molecular, phylogenetic, and ecological data and tools are also used, so the field is quite multidisciplinary. The tendency is to integrate data from palaeontology, molecular, and morphological studies to get as close as possible to the “holy grail of snake evolution”—the earliest snake ancestor (Caprette et al., 2004; F. O. Da Silva et al., 2018; Hsiang et al., 2015).

Because limblessness and the presence of an elongated slender body have had a pervasive effect on snake biology, snakes have proved to be excellent animals for studying extreme or unusual adaptations in functional morphology (Jayne et al., 2015; Krishnan et al., 2014; Moon et al., 2019; Phadnis et al., 2019; Young et al., 2004), physiology (Goris, 2011; McCue et al., 2012; Secor, 2008; Secor & Diamond, 1998; Yoshida et al.,

2020), and behavior (e.g., Catania, 2010; Jayne et al., 2002; A. K. Miller et al., 2015; Shine, 2012). However, research using snakes as models is still lagging behind the research on several other groups of vertebrates in terms of number of published papers (Figure 1); snakes, together with crocodylians and salamanders, constantly suffer from “taxonomic chauvinism” (Bonnet et al., 2002) or, simply speaking, plain disparagement. Laymen have frequently asked me why I wanted to study snakes, as they are “awful and dangerous animals.” Such questions and statements from the general public presumably have indirect effects on the funding of research. Contrary to the low popularity of snakes in research per se, biochemistry, molecular biology, and pharmacology of snake venoms have long been active areas of research (Akef, 2019; Perez-Peinado et al., 2020; Saviola et al., 2014). These areas are popular because snake venoms are a rich source of potentially useful substances for pharmaceutical and/or biotechnological industry. This problem is complex, going beyond the scope of this article and probably deserving of a detailed sociological analysis.

Although snakes can be excellent research subjects in some areas, they can be problematic in others; their morphological, physiological, and behavioral uniqueness is a double-edged sword. For example, they can be difficult

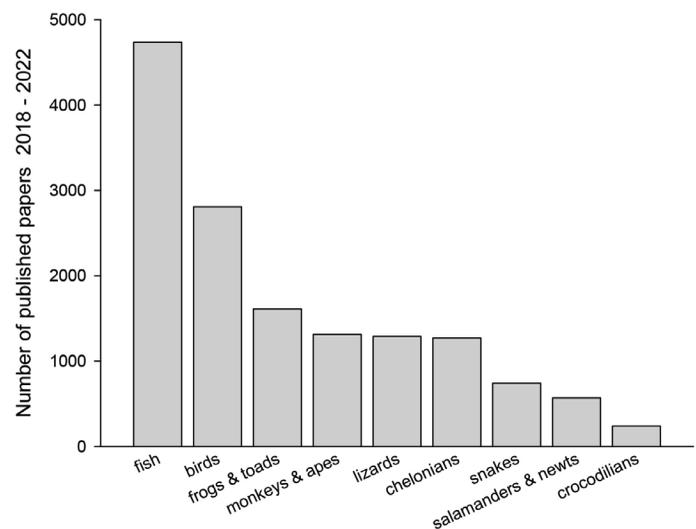


Figure 1. The number of published papers for the selected groups of experimental animals in Web of Science categories that may be relevant in behavioral research. The following were the search parameters. Search field: Title; Publication years: January 1, 2018–December 31, 2021; Document type: Article; WoS categories: Behavioral sciences, Biological psychology, Biology, Ecology, Evolutionary biology, Experimental psychology, Neurosciences, Physiology, Psychology, Zoology. Note that the literature search was not stringent and as detailed as in Szabo et al. (2021; i.e., articles that may be irrelevant to behavioral research were not searched for and removed from the listings). The whole search was done only to show the general trend.

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to train using standard reward paradigms because they need to eat so infrequently. Failure to recognize this and to match the right species to the right problem frequently results in meager scientific data and disappointment (Seigel, 1993). In the following sections, I present the sensory and cognitive capacities of snakes to outline what one needs to know in order to study snake behavior and in order to paint a picture of the type of comparative cognition research questions that would benefit from the study of snakes.

The Sensory World of Snakes

Normal behavior of animals depends on continuous gathering of information from the external and internal environments via sensory organs; processing sensory information in the central nervous system, sometimes using the stored information of past experiences as a modulator; and generating the appropriate motor output (Randall et al., 2001). Snakes, as vertebrates, are no exception. As noted previously, their body shape has affected many aspects of their biology, and different senses are involved, to varying degrees, in shaping their behavior. The most important modes of sensory perception in snakes are vision *sensu stricto*, visual thermoreception (in boids, pythonids, and crotalines), olfaction (vomeroolfaction), and parts of somatosensation (touch; Ford & Burghardt, 1993). Unfortunately, we know much less of snakes’ auditory, nasolfactory, and gustatory perception, as they appear to contribute much less to some aspects of ophidian behavior (e.g., social interactions) than the aforementioned senses. But this assumption may also stem from our negligence to assess these fields appropriately and/or study them using innovative techniques. These approaches may yield novel, perhaps unexpected, information about snake perceptual abilities and behavior (Young, 2003).

Vision “Sensu Stricto”

The eyes of snakes, in their general anatomy, resemble the eyes of other vertebrates. Snakes have camera-type eyes, with lenses that focus light on the pigment epithelium of the retina. Photoreceptors, by the process of chemical phototransduction, transduce light into electrical signals, which are then transmitted to the brain. Although snakes share many features of their visual anatomy and physiology with other vertebrates, in terms of specific features (e.g., lens spectral transmission, retinal anatomy, visual pigment spectral specificity and evolution), they are a very diverse group of vertebrates, perhaps the most complex one (Simões, Sampaio, Douglas, et al., 2016).

These specific features reflect the ecological situation in which snake eyes have evolved (Y. Liu et al., 2012).

The eyes of most snakes are placed laterally and allow roughly 30° to 40° of binocular overlap, that is, stereoscopic vision. However, four genera of arboreal snakes (*Ahaetulla*, *Oxybelis*, *Thelotornis*, *Uromacer*) have stereoscopic vision of up to 46°. They live in a complex environment in which judging of distances is of crucial importance. These snakes have thin, elongated bodies and heads; their heads have eyes with a horizontal keyhole-like pupil. Deep grooves run from the anterior part of the eye to the tip of the snout on each side of the head. The combination of horizontal keyhole pupil and grooves extend the visual field without obstructing the extent of periscopy (Henderson & Binder, 1980). The lens is placed posteriorly in the eye (Figure 2), leaving the anterior part aphakic (lensless). When a snake focuses, it moves the lenses into aphakic space. This action widens the angle of stereoscopic vision (Lillywhite & Henderson, 1993).

Snake eyes are covered with transparent skin called the spectacle or brille. During the process of ecdysis, snakes shed it with the rest of the skin. The spectacle is, like the rest of the skin, vascularized. The blood flowing through it is strictly controlled, but it is not clear how this affects vision (van Doorn & Sivak, 2013).

The vertebrate cornea protects the lens and serves as the main refractive body of the eye, which is in contact with the environment. In snakes, it is covered with the spectacle, and between them is a space filled by subspectacular fluid that allows free movements of the eye. Because this

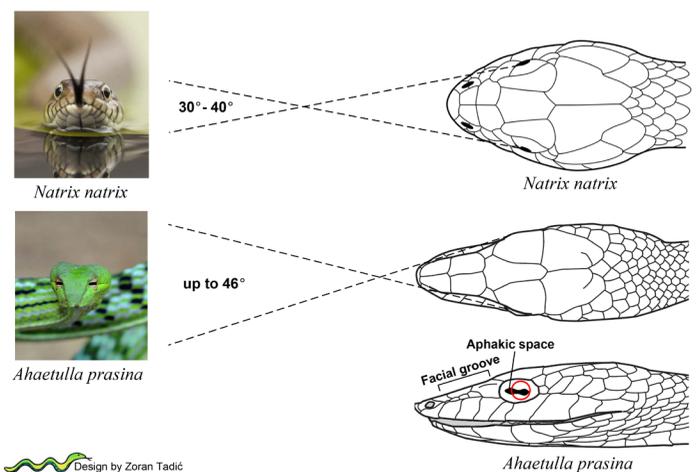


Figure 2. Eye placement and the visual fields in highly arboreal and terrestrial snakes. The figure was composed by the author using several sources: Photos of *N. natrix* (by Jamie Hall), *A. prasina* (by Arif Supriyadi), and drawing of *N. natrix* head (by Valentina Moraru) are from Shutterstock. Drawings of *A. prasina* head are slightly modified from Miralles and David (2010). Red circle marks position of the lens.

fluid has the same refractive index as aqueous and vitreous humor, it has long been thought that the cornea does not exert much influence on snakes' vision. However, recent research in functional morphology suggests that this may not be the case (M.-A. O. Da Silva et al., 2020).

Visual accommodation of the vertebrate eye depends on the accurate projection of the lens-inverted image on the retina. Because animals have to see objects clearly at various distances, the lens must focus accurately and project a clear picture on the retina. Birds and mammals accommodate by changing the compliant lens diameter using the contraction of ciliary muscles. In snakes, however, the lens is noncompliant and cannot change diameter. Therefore, snakes focus by contracting muscles at the base of the iris. This action raises pressure in the posterior compartment with the vitreous body and pushes the lens forward (Underwood, 1970). This method of accommodation is not very efficient, as the noncompliant lens cannot move much. Therefore, we assume that the vision and visual perception of snakes is quite limited or, at least, not comparable in accommodative abilities to that of lizards and other amniotes. The aquatic medium presents special problems, as water has a high refractive index compared with the surface of the eye, and the eyes would need to accommodate to the extreme to cope with this problem. Because accommodation of the eye in snakes is limited, using eyes underwater probably results in blurred vision, like in humans. However, several semiaquatic snakes can focus clearly under water; exactly how this is achieved remains unknown (Schaeffel & de Queiroz, 1990; Schaeffel & Mathis, 1991). Sea snakes are said to overcome this problem by constricting the pupil to a pinhole size (Underwood, 1970). Lenses also show evolutionary adaptation to various ecological contexts. The lenses of diurnal species filter out shorter wavelengths, whereas nocturnal species allow UV to reach their retinas, where it may aid vision at night (Simões, Sampaio, Douglas, et al., 2016).

Snake retinas, like those of most vertebrates, contain two types of photoreceptors: rods and cones (Yokoyama & Yokoyama, 1996). Rods are more sensitive and are used for vision in dim light. Cones are used for color vision in daylight. The majority of snakes have retinas consisting of rods and cones (Underwood, 1970). Such duplex retinas are considered to be an ancestral trait but, as one evolutionary hypothesis suggests a subterranean origin of snakes, it is thought that their retinas have been populated with more cones. Diurnal snakes, such as terrestrial elapids and colubrids, have a round pupil and retinas consisting mostly of cones. Some, like the common garter snake (*Thamnophis sirtalis*), have all-cone retinas. Fossorial, crepuscular, and

nocturnal snakes (e.g. some colubrids and vipers) usually have slit pupils and retinas that have mostly rods.

In his influential book *The Vertebrate Eye and Its Adaptive Radiation*, G. Walls (1942) proposed the “transmutation” theory of photoreceptor evolution. According to this hypothesis, the repopulation of the retina with cones did not involve the extinction of rods and the reevolution of a new cone types but by evolutionary “transmutation” of one type of photoreceptor to another. For years, the hypothesis had remained experimentally untested, until the beginning of 21st century when it was shown to occur in geckos and caenophidian snakes (Bhattacharyya et al., 2017; Schott et al., 2016; Zhang et al., 2006). However, the retinas of haenophidian snakes do not show such a phenomenon (Davies et al., 2009).

The snake retina has many morphological subtypes of photoreceptors, and they differ between species and between snake families and subfamilies. Snakes have four photoreceptor patterns/complements. Some snakes have the typical “viperine pattern” of three cone subtypes and one rod type, which is considered ancestral and so named because it is characteristic of viperid snakes. The “Natriicine pattern” consists of three cone subtypes and no rods and is a hallmark of diurnality. And “three cone subtypes, with rod-like outer segments” and “transmuted rod-like cones” types are characteristic of nocturnal snakes (Simões, Sampaio, Loew, et al., 2016; Walls, 1942).

Of five possible vertebrate visual pigments (RH1, RH2, SWS1, SWS2, and LWS), snakes have lost two in cones (RH2 and SWS2); thus essentially they have dichromatic color vision. The photopigment combination RH1, SWS1, LWS is thought to be ancestral and is present in all snakes. Gene sequencing of snake opsins (the protein part of photopigment) has revealed exceptional complexity in the evolution of visual systems of snakes. Readers interested in this complex subject should consult the work by Simões and Gower (2017) and the references within.

It is interesting to note that several species of sea snakes have photoreceptors on the skin of their tails. These photoreceptors lack opsins and use a different phototransducing mechanism, using melanopsin. Zimmerman and Heatwole proposed that these caudal cutaneous photoreceptors are used to detect whether the whole body or the tail has been concealed among corals (Crowe-Riddell et al., 2019; Zimmerman & Heatwole, 1990).

Although vision plays a very important role in foraging, some snakes can accommodate to its loss, as exemplified by tiger snakes (*Notechis scutatus*) living on the Carnac Island, near the shore of Western Australia. Some of these highly venomous snakes, mostly males, are

blind. The blindness is induced by the defensive pecking by seabirds whose chicks the snakes catch in the nesting burrows. Although one may suppose vision loss to be a death sentence for the snakes, it is not so, as the majority of blinded snakes are in very good body condition. It turns out that these blind snakes continue to feed on chicks in the nesting burrows, leading to the hypothesis that the eyes are less important in the dark burrow than the chemical senses on which blind snakes probably rely in this foraging situation. This hypothesis was tested in the laboratory and in a field situation: Blindfolded tiger snakes had difficulties in catching moving prey in the laboratory, whereas free-ranging blinded snakes on Carnac Island took almost exclusively seagull chicks. In opposition, normal snakes also took fast-moving prey, such as lizards and small rodents (Aubret, 2016; Aubret et al., 2005; Bonnet et al., 1999).

Thermal Vision

Some snakes, such as pit vipers (e.g., rattlesnakes, lanceheads, many Asian crotaline snakes) and some boas and pythons, possess specialized thermosensitive organs. This ability to detect heat has evolved independently in several taxa of vipers and boas and pythons. In vipers, these organs are situated in paired facial or loreal pits (hence the name *pit viper*), but in boas and pythons they are on and between the labial scales, respectively (Noble & Schmidt, 1937; Warren & Proske, 1968). The facial pit of the pit vipers is a chamber in which a suspended thermosensitive membrane separates it into an anterior and posterior compartment. The thermosensitive membranes of boas and pythons are, on the other hand, placed directly on the scales or between them (Molenaar, 1992). Facial pits, probably because of the specific anatomical layout, are more sensitive than similar organs in boas and pythons, able to detect moving prey up to 100 cm away, compared to about 30 cm in boas and pythons (Ebert et al., 2007; Ebert & Westhoff, 2006). Thermosensitive membranes do not have specialized thermoreceptor cells but are innervated directly by the opthalmic and maxillary branch of the trigeminal nerve (Lynn, 1931). Membranes of these neurons have special ion channels called TRPA1 (TRP stands for transient receptor potential) channels, which are activated by heat (Gracheva et al., 2010; Panzano et al., 2010). They belong to the family of TRP proteins, which have a wide range of functions (Gracheva & Bagriantsev, 2015; Islam, 2011). Thermosensitive membranes are highly vascularized. This allows oxygen provision to the membrane as well as the cooling of the membrane and its reversion to the normal state, and thus it

prevents afterimage formation after the scanned object is removed (Goris et al., 2003). Membranes in the facial pits of pit vipers can also be cooled using evaporative water loss during increased breathing, and their sensitivity can be increased this way (Cadena et al., 2013).

Nerve fibers from the thermosensitive membrane project to the optic tectum. This part of the brain, apart from thermal, also gets motor, auditory, and proprioceptive information. The optic tectum integrates visual and thermal information and relays it to the forebrain. Therefore, the snake obtains an integrated visual and thermal picture of its surroundings, ranging from the IR spectrum upward (Berson & Hartline, 1988; Hartline et al., 1978; Newman & Hartline, 1981).

The facial pit actually acts as a pinhole camera, but its sensitivity is poor. The diameter of the pit, together with its poor heat conduction and small size, produces an image on the membrane that is of extremely low contrast and resolution. The nervous system may be involved in sharpening the resultant image, and the integration of visual and thermal information may also play this role, but it is unknown to what extent these processes occur (Bakken & Krochmal, 2007).

Snakes use thermosensitive organs to target warm-blooded prey, although they probably do not evaluate animals on the basis of their body temperature alone. It seems that the IR image of the prey is sufficient for accurate targeting and the initiation of a predatory attack, as congenitally blind rattlesnakes and ones that have been temporarily blinded in the laboratory strike at prey accurately (Kardong & Mackessy, 1991; Schraft et al., 2018).

Although thermoreceptive organs in snakes are always thought to have evolved for prey capture, their usage in prey detection may have occurred later in their evolutionary development. Instead, facial pits may have evolved because of the need for thermal regulation. When tested for thermoregulatory movements, pit vipers were able to rely on their pits to accomplish these, whereas pitless vipers were unable to do so (Krochmal et al., 2004). Pit vipers can also use the thermal profile of the environment to select ambush sites (Schraft et al., 2019). Unfortunately, we know nothing about thermoreceptive organ use during thermoregulation in boas and pythons.

Although today they are regarded as an extension to ordinary vision, thermoreceptive organs do have limitations. For instance, they cannot be used for navigation, as they detect only the IR spectrum of light and this information, apparently, is not enough to navigate successfully (Schraft & Clark, 2019).

Chemical Senses (Olfaction)

Vomerolfaction

One of the most prominent behaviors that snakes exhibit is tongue-flicking. In fact, this behavior has become so associated with snakes that it has created the proverbial forked “serpent’s tongue” of many folktales, myths, and even modern fiction. However, the tongue is of crucial importance in the lives of snakes. One tongue-flicking bout consists of protrusion of the tongue, moving it up and down several times in oscillatory manner, and its retraction back to the mouth. During oscillatory movement, the tongue samples chemicals in the air or on the objects it has touched and brings them to the mouth for chemical analysis. The tongue itself is not a chemical probe, just a transfer tool as sampled chemicals are transferred to the vomeronasal or Jacobson’s organ (VNO; Parsons, 1970). The VNO is an organ situated near the nasal cavity and is connected to the mouth with narrow ducts. These ducts open on an anterior palate. Neurons from VNO olfactory epithelium project fibers to the accessory olfactory bulb. From there, vomerolfactory information goes to the *nucleus sphericus*, lateral amygdala, and lateral cortex, which is thought to be the center for processing of this information. It is also possible that vomerolfactory and nasolfactory information is integrated in the lateral cortex (Lanuza & Halpern, 1997). From the lateral amygdala, neurons project to the lateral posterior nucleus of the hypothalamus and continue to the hypoglossal nucleus (NXII) of *medulla oblongata* (Halpern & Martinez-Marcos, 2003). Axons from this nucleus form the 12th cranial nerve, which innervates tongue and controls tongue-flicking. The detailed description of the VNO and the associated neural structures can be found in two comprehensive reviews by Halpern (1987, 1992).

The tongue has two tines that can separate for a variable distance during odorant sampling, giving it its “forky” appearance. It is thought that tines have evolved to facilitate chemical trail edge detection by tropotaxis (Schwenk, 1994). However, rattlesnakes (*Crotalus oreganus*) in which vomeronasal nerves were unilaterally surgically severed failed to show disrupted tropotactic chemosensory search, suggesting that other factors may be involved in the evolution of anterior tongue bifurcation in snakes (Parker et al., 2008). It has long been thought that the sampled chemicals are delivered to the VNO directly, the tips of the tines being pushed into the VNO ducts. However, tips of the tines, in most snakes, are too thick to enter the ducts, let alone penetrate the VNO chamber, so other hypotheses were proposed for the transfer of chemicals from tongue to the VNO (Young, 1993). The hypothesis that was the most

acceptable from an anatomical/morphological point was the “suction hypothesis,” according to which the sampled chemicals are sucked into the VNO by a vacuum created by tongue and/or associated structures. Gillingham and Clark (1981) suggested that the elevation of the anterior processes of sublingual plicae may be responsible for the transfer of chemicals, as they might promote creation of the vacuum in the VNO. However, more recent research failed to confirm their role in it (Halpern & Borghjid, 1997). So the exact mechanism of the transfer of chemicals from tongue to the VNO remains unknown. The frequency and duration of tongue-flicking may be mediated by behavioral and ecological context (Baeckens et al., 2017; Cruz et al., 1987; Gove & Burghardt, 1983).

As snakes are very chemoreceptively-oriented animals, and tongue-flicking is of pervasive importance in many aspects of their behavior (Ford, 1986; Gabriot et al., 2012; Halpern & Kubie, 1984; Mason & Parker, 2010; Richard et al., 2018; Scott et al., 2013; Stark et al., 2011; Stone & Holtzman, 1996). One of the most studied chemoreceptive behaviors in snakes is strike-induced chemosensory searching (SICS). Because of their specific predatory behavior (i.e., envenoming strike), SICS is almost a distinguishing feature of viperid snakes, but other snakes also express it (Burghardt & Chmura, 1993; Chiszar et al., 1977, 1982; Chiszar, Radcliffe, et al., 1980; Cooper, 1991; Cruz et al., 1987). After the snake’s predatory envenomating strike, the bitten animal usually wanders off some distance but soon succumbs to the action of venom. The snake usually waits for some time and then starts to search for the prey using the chemical trail left by the prey. When the snake starts searching and following the chemical trail, the frequency of tongue-flicking increases dramatically. It has been shown that during the predatory strike and brief contact with the prey, a chemical search image forms in the nervous system, which is subsequently used for chemosensory searching (Chiszar et al., 1985; Melcer & Chiszar, 1989). Recently, it was discovered that rattlesnakes may use disintegrins (venom-specific proteins) to relocate stricken prey (Saviola et al., 2013). A comprehensive coverage of significance of SICS in the predatory behavior of rattlesnakes is available (Chiszar et al., 1992).

Because vomerolfaction plays an important part in various aspects of their life, the loss of vomeronasal function can have disastrous consequences on snakes. Although in pit vipers, in the initial phases of predatory attack, both ocular and thermal vision play important roles, it seems that the main mediator of the overall response is vomerolfaction. In one study, Prairie rattlesnakes (*Crotalus viridis*) that had surgically sutured VNO ducts failed to

attack prey and emitted fewer tongue flicks as compared with the control animals (Graves & Duvall, 1985). Also, Northern Pacific rattlesnakes (*Crotalus oreganus*) with sutured VNO ducts exhibited fewer strikes and their chemosensory trailing and swallowing ability was completely suppressed (Alving & Kardong, 1996). This indicates that vomerolfaction plays a crucial role in predatory behavior of rattlesnakes, acting as a releaser of predatory attack and principal mediator of trailing in the poststrike environment.

Nasolfaction

As compared with vomerolfaction, nasolfaction research in snakes has been severely neglected, and there is an incredible paucity of literature on this subject. Nerve fibers from nasal olfactory epithelium project to main olfactory bulb and, from there, to the olfactory nucleus, olfactory tubercle, and lateral pallium (lateral cortex; Halpern, 1976). It is possible that the vomerolfactory and nasolfactory information integrate in the ventral cortex, as they converge there, but it is not known to what extent and how snakes use this integrated information (Lanuza & Halpern, 1997). Molecular studies of olfactory receptor pseudogenes in four species of snakes revealed they are present in only one species (copperhead). This indicates that snakes may be using nasolfaction more than is usually assumed (Byerly et al., 2010). Similar molecular studies on sea snakes showed that completely aquatic, viviparous sea snakes have a smaller number of olfactory receptor genes, as compared with oviparous sea snakes that venture on land during egg laying (Kishida & Hikida, 2010), suggesting that snakes do use nasolfaction in terrestrial environments. However, nasolfaction remains one of the less explored areas of snake sensory perception.

Touch

Snakes are limbless, and their body is in more intimate contact with the environment, as compared with most other tetrapods. Consequently, they must have a well-developed sense of touch, as this is important not only for locomotion but also during other activities such as predation (e.g., during constriction). Touch needs to be sensitive to be useful, as snakes are covered with scaly skin, which diminishes its sensitivity. Although the morphology of various skin mechanoreceptors has been known for a long time, we do not know much about how their physiology interacts with the central nervous system to coordinate behavior. However, from certain behaviors we hypothesize that thigmoreceptors are important in snakes' everyday lives. As this review is on how sensory physiology and reception reflect on behavior, I do not describe the

morphology of skin receptors and their response to various experimental stimuli in detail. Detailed descriptions of external and internal somatosensory receptors can be found in several good reviews (Crowe, 1992; von Düring, 1973; von Düring & Miller, 1979). Skin receptors include free nerve endings, tubercles, papillae, and scale sensillae (Jackson & Sharawy, 1980; Proske, 1969; Young & Wallach, 1998). Sensory information from them is projected to the midbrain (i.e., optic tectum), which processes it (Hartline, 1971a; Ulinski et al., 1992).

Although snakes extensively rely on thigmotaxis in many aspects of their lives, this information is probably integrated with other sensory information to express normal behavior. Red spitting cobras (*Naja pallida*) used transparent Plexiglass hiding boxes, indicating that thigmotactic cues alone are sufficient to express hiding behavior. However, when the snakes were tested in simultaneous discrimination tests, dark hiding boxes were always preferred to the Plexiglass ones, indicating that thigmotaxis plus vision are typically used to find appropriate hiding places (Chiszar et al., 1987).

Snakes also show unexpected behaviors in which mechanoreception is thought to be involved. Sea kraits (*Laticauda spp.*) disappear from their habitat about a day before the onset of hurricane. They presumably sense a sharp fall in barometric pressure, and some kind of mechanoreception/pressure reception is probably involved (Y.-L. Liu et al., 2010). Shaw's sea snake (*Lapemis curtus*) are sensitive to low-frequency water movements, which they may use in detecting fish (Westhoff, Fry, & Bleckmann, 2005). Snakes that use constriction in subduing prey do this by inducing cardiovascular collapse by strong pressure (Boback et al., 2015). It is of crucial importance for the snake to know when the constricted animal is dead, as prematurely released prey may either run away or retaliate and injure the snake. Constriction is also energetically costly (Canjani et al., 2002); because of this, snakes can modulate the duration of constriction by sensing the prey's heartbeat (Boback et al., 2012). They probably do this by employing some kind of surface or internal mechanoreceptor to sense cardiovascular function of the prey and readjust coils and pressure (Moon, 2000). The tentacled snake (*Erpeton tentaculatum*) lives in Southeast Asia, is completely aquatic, and exploits fish escape responses to catch them (Catania, 2009; Murphy, 2007). This snake was thus named because of two soft projections at the tip of the snout, the function of which has long been debated. These projections (called tentacles) are, in fact, sensitive mechanoreceptors, innervated by the ophthalmic and maxillary branch of the trigeminal nerve. The mechanosensory

information is projected to the optic tectum. Visual information is enough to initiate predatory strikes, but under infrared light in darkness, predatory strikes are still accurate, suggesting that the appendages serve to complement visual information and enhance prey location in conditions of dim light (Catania et al., 2010).

Hearing

For a long time, snakes were presumed to be deaf and unable to perceive any sounds. This notion was supported by the fact that they have no externally visible outer ear structure. In the middle ear, there is no Eustachian tube and there is only one ossicle—the *columella auris*, which is thought to be an evolutionary equivalent of stapes (Wever, 1978). Therefore, the external ear in snakes is nonexistent, and the middle ear is reduced. The proximal end of the columella has an extended footplate that touches the oval window (*fenestra ovalis*) of the fully functional cochlea (the inner ear). The distal end of columella is, via cartilaginous element, articulated to the quadrate bone. This bone is crucial in transferring vibrations to cochlea via the columella. Although the exact mechanism of detection of airborne sounds is unknown, some experiments suggest that airborne sounds induce head vibrations that are transferred via the quadrate bone to the columella and cochlea. So it may be that airborne sounds are detected as vibrational stimuli (Christensen et al., 2012). Also, it is not known how snakes locate the source of airborne sounds and groundborne vibrations.

The first physiological studies on snakes auditory abilities showed that not only are snakes not deaf but they can detect airborne sounds (Hartline, 1971a, 1971b; Hartline & Campbell, 1969). Moreover, these studies confirmed that snakes also have two physiologically separate auditory systems for the detection of vibratory stimuli. The cochlear system (in the inner ear) is the more sensitive of the two, but it also has a reduced range of frequencies. The other system is somatosensory and has lower sensitivity but greater frequency range (Hartline, 1971b). The latter presumably uses somatic receptors of some kind. However, the nature of these receptors and the interaction between these two systems in the ophidian hearing is still not fully understood and the neural mechanisms of somatic and cochlear information integration in the formation of auditory picture remain unknown.

The auditory nerve pathway from cochlea to brain is also poorly understood, and only one study used modern techniques (M. R. Miller, 1980). Most modern neuroanatomical studies are done on lizards and assume lizards and snakes have the same auditory neuroanatomy without any

experimental evidence that the same neuroanatomical features exist in snakes. The auditory/vibrational information is conveyed to the telencephalon, but nothing is known about the size and location of the auditory part of the telencephalon in snakes.

As previously mentioned, snakes can detect airborne and vibrational auditory stimuli and can put them in a behavioral context. When Western diamondback rattlesnakes (*Crotalus atrox*) were tested to various airborne sounds in an isolation chamber, they responded defensively to them (Young & Aguiar, 2002). Groundborne vibrations in olfactory-denervated temporarily blinded Saharan sand vipers (*Cerastes cerastes*) resulted in predatory behavior (Young & Morain, 2002). The maximum distance for the detection of mouse groundborne vibrations is about 128 cm in Saharan sand vipers, so their usefulness for the detection of predators may be limited. Recent research shows that sea snakes have underwater hearing but they are much less sensitive to underwater sounds compared with fishes and sea turtles. It is also not known how underwater hearing affects a snake's behavioral ecology, as the study is purely physiological (Chapuis et al., 2019).

Auditory physiology and perception in snakes is a poorly explored area, and many observations have not been experimentally tested. Consequently, a comprehensive review of snake bioacoustics exists, which despite its respectable age (20 years old!) is still up-to-date (Young, 2003).

Cognitive Abilities

A single definition of animal cognition does not exist; the definitions vary widely according to their stringency. To cite a very stringent definition, animal cognition is the ability of an animal to mentally assess a current behavioral situation, to contemplate past experiences, to predict the future consequences, and to act accordingly (Breed & Moore, 2016). However, few animals are known to meet this criterion. A more relaxed definition is proposed by Shettleworth (2001): animal cognition “includes all ways in which animals take in information through the senses, process, retain and decide to act on it” (p. 277). Cognition is closely tied to learning, as animals must collect and store information to behaviorally express it in the appropriate spatio-temporal situation. Cognition can also affect fitness, as it can mediate reproductive behavior, foraging, defense, spatial distribution, and migration (Shettleworth, 2010). The first comprehensive review on learning in reptiles was written 46 years ago (Burghardt, 1977), and a recent one (Szabo et al., 2021) provides an extensive overview

of reptilian learning abilities and essentially serves as an update of the former.

A glimpse of the recent review on reptile learning shows that snakes, as model animals in cognition research, are poorly represented (see Figures 1 and 2 in Szabo et al., 2021). In recent years, we have seen a surge in interest in reptile cognition. However, this interest is focused mainly on the reptilian taxa other than snakes, such as lizards and chelonians (Matsubara et al., 2017; Wilkinson & Huber, 2012). As the introduction states, there are probably multiple, complex reasons why this is so, ranging from sociological to biological. Yet if we take a general look at the research on snakes, we can see that snakes are good models in functional anatomy/physiology, behavior (especially in chemical ecology and perception), and evolution research. The extreme adaptations in snakes (e.g., body form, lack of the external ear, relatively poor visual accommodation, infrequent consumption of large meals, and the extreme inactivity in some species) seem to be a blessing for one type of research but a curse for another type. It should also be mentioned that snake cognition research is lagging behind because, in many cases, traditional methods of cognition research used in mammals and other reptilian taxa are employed on snakes, often with disappointing results. The state of the science of snake cognition is nicely exemplified by the fact that a recently published book on laboratory methods in animal cognition contains only a two-page box insert on snake cognition, inside the chapter on lizard cognition (Bueno-Guerra & Amici, 2018).

Social Behavior

Still today, snakes are presumed to be the least social of all reptiles, restricting their social contact with the conspecifics during hibernation, antagonistic interactions, and courtship/mating. Reptiles in general are not favored experimental subjects in comparative social behavior research, and there is no clear reason why this should be so, at least in reptilian taxa other than snakes (Doody et al., 2013). The first experiments on snake social aggregation behavior were completed in the mid-1930s (Noble & Clausen, 1936). The methods used to achieve sensory deprivation are unacceptable by today's standards (e.g., severing the tongue), and the stimulus to induce aggregation was quite unnatural (i.e., shaking the cage). The aim was to test which sensory cues mediate aggregation behavior in two adult North American natricine snake species (*Storeria dekayi* and *Thamnophis sauritus*). Noble and Clausen concluded that vision is the primary sense that triggers aggregation, whereas olfaction is the secondary and the tongue plays no part in mediating aggregation. In opposition, species

identification is accomplished by olfaction and vision has the secondary role. Because of the unnatural environment, stimuli and animal manipulation technique, the results of these experiments remain controversial.

Social aggregations of snakes have been extensively studied in garter snakes and rattlesnakes. In garter snakes, aggregation behavior is influenced by diet, relatedness, competition, age, and personality (e.g., boldness and willingness to socialize) of individual animals (Burghardt, 1983; Lyman-Henley & Burghardt, 1994; Skinner & Miller, 2020; Yeager & Burghardt, 1991) and is probably additionally mediated by aggregation pheromones (Graves et al., 1991). Rattlesnakes use communal dens in which they aggregate for hibernation, and females may use them as communal rookeries (Butler et al., 1995). Because chemical senses play a pervasive role in the biology of snakes (see the previous section on vomerolfaction), rattlesnakes may use chemical trails of conspecifics to locate such dens (Brown & MacLean, 1983; Graves et al., 1986; Muellman et al., 2018). The use of chemical information by rattlesnakes is not limited to den location. The males may use it to locate females (Coupe, 2002), or it may be used as a tag, indicating areas where food is abundant (Clark, 2007). Social behavior has also been observed in captive indian pythons (*Python morulus*) and wild big-eyed pitvipers (*Trimeresurus macrops*), but nothing is known about frequency of such behavior in these species in the wild (Barker et al., 1979; Barnes et al., 2019).

Kin Recognition

The only studied snakes that exhibit kin recognition are rattlesnakes, although this phenomenon may have gone unnoticed in other snakes (Clark, 2004; Clark et al., 2012). This behavior could be adaptive, as kin aggregation may, at least theoretically, enhance antipredator defence via a dilution effect (Lehtonen & Jaatinen, 2016). Related snakes may also be able to orchestrate antipredator behavior more efficiently (Duvall et al., 1985; Graves & Duvall, 1988). Rattlesnake neonates usually stay near their mother until their first molt (ca. 10 days), which gives them a fair degree of protection. Mothers and even fathers can actively protect them (Amarello et al., 2011; Hewlett & Schuett, 2019). Such maternal attendance could affect subsequent development of specific affiliative behavior (Hoss et al., 2015). Neurophysiological foundations of this behavior remain unknown, but they may be related to neuroendocrine function, as blockage of the neurohormone vasotocin receptor disrupts maternal behavior in the pigmy rattlesnake (*Sistrurus miliarius*; Lind et al., 2017). Intuition suggests that chemical information could mediate the process of kin

recognition and maternal affiliation, but tactile and visual stimuli may also be implicated in the process.

Communication

Communication is a complex process of sending information to other individuals and/or receiving and processing information gathered from other individuals and adjusting behavior using these cues (Bradbury & Vehrencamp, 2011). Snakes communicate with conspecifics mainly using chemical trails and touch; visual communication is noted only in male combat (Doody et al., 2021). However, visual communication among conspecifics and heterospecifics may be more widespread than currently believed, as many snakes have big eyes; large eyes, apart from foraging, could be used in assessing visual communication signals.

Chemical trails left by conspecifics have an important role in reproductive and aggregation behavior in snakes (Ford, 1986). As previously mentioned, rattlesnakes come to communal hibernacula before winter, and the same places are frequently used as communal rookeries. Individual snakes use chemical trails left by conspecifics to utilize such places (Butler et al., 1995). Therefore, the location of hibernaculum/rookery is chemically communicated to the conspecifics. At the denning place, communication can be olfactory but can be expressed via tactile signals, as snakes lie coiled around and at the entrance, with their bodies intertwined. At this time, we can only speculate about the nature of exchanged signals and messages at these places. Tactile signals and visual signals emitted and received before and during male combat in viperid snakes may have a long-lasting effect on their subsequent reproductive success. During mating season, male copperheads (*Agkistrodon contortrix*) usually engage in ritualized combats typical of many viperid snakes. Males that have lost staged fights in the laboratory exhibit typical winner–loser effects: If contested with an opponent that is about 10% smaller, the males will always lose the fight if they lost two previous fights (Schuett, 1996, 1997).

Contrary to the cryptic intraspecific messages, interspecific messaging in snakes is well documented and comprises mainly antipredatory displays (Greene, 1988). The arsenal of antipredatory signals ranges from hissing, inflating the body, mouth gaping in various modes, emitting sizzling sounds by rubbing ridged body scales (genus *Echis*; Spawls & Branch, 1995), rattling by rattlesnakes (*Crotalus* and *Sistrurus*; Kissner et al., 1997), hood spreading and venom spitting by cobras (genus *Naja* and related genera; Westhoff, Tzschatzsch, & Bleckmann, 2005; Young et al., 2009; Young & Kardong, 2010), and

body arching and jerking in North American crotaline and natricine snakes when faced with an ophiophagous snake (Carpenter & Gillingham, 1975; Weldon, 1982; Weldon & Burghardt, 1979). In all these behaviors, the snake must recognize the incoming object, identify it as a potential threat, and launch a behavior that is aimed at deterring the potential attack. The complexity level of assessing the threat and consequent antipredatory behavior can be best exemplified by venom-spitting behavior used by some cobras to discourage predatory attack. They eject either a thin jet or a spray of venom at high pressure and speed from their fangs. The venom is aimed at the face and is a potent irritant that can temporarily or permanently blind the attacker (Berthé et al., 2013). High-speed filming has shown that spitting cobras track the movement of the eyes of the attacker, up to the point when spitting is triggered, mainly by the action (e.g., small movements) of the attacker. From this point on, the cobra does not track but predicts the position of the eyes of the attacker, about 200 ms in advance (Westhoff et al., 2010). Such a sequence of events presumably requires complex information processing in the nervous system and, consequently, sophisticated cognition of the target and its movement in space to achieve an acceptable hit.

Spatial Orientation and Navigation

Orientation and navigation in nature is essential to finding food, shelter, and mating partners. Unfortunately, a small number of snake species have been tested for spatial learning and navigation. Juvenile corn snakes (*Pantherophis guttatus*) successfully learned to navigate a Barnes maze and solve an escape task (Holtzman et al., 1999). Adult corn snakes were tested in a modified Barnes maze, with the hiding boxes instead of holes and an intramaze visual cue serving as a landmark. They also showed spatial learning abilities and, when the visual cue was moved to another location, they changed their behavior accordingly and searched for the shelter in the area predicted by the cue (Holtzman, 1998). Juvenile spotted pythons (*Antaresia maculosa*) were also tested in a Barnes maze, similar to the one used with juvenile corn snakes. However, the pythons were not as successful in finding the goal as the juvenile corn snakes, and only half of them were able to solve the task. Stone et al. (2000) proposed that these differences in the ability to solve the spatial tasks may be due to their circadian activity; the spotted pythons are nocturnal and show little exploratory activity during trials potentially because they were conducted during the day. The experiments just described were done in plain testing arenas, with almost no other visual stimuli than those used

in the experiments. However, the most spectacular results on navigational abilities of snakes were obtained in wild Burmese pythons (*Python bivittatus*) in the Everglades National Park in the U.S. state of Florida. Of 12 adult pythons, six were translocated more than 20 km from the place of initial capture. Five out of the six returned within 5 km of the site of initial capture, suggesting they possess a map and a compass sense (Pittman et al., 2014).

Self-Recognition

If and how animals can recognize themselves as individuals has always been a hotly debated issue among both scientists and laymen. There is a paucity of research on reptile self-recognition, as compared with the research using mammals and birds. Snakes are especially unlikely to be tested in classical self-recognition tests (e.g., the mirror test, detour, gaze-following) because these procedures are only partially successful or do not work at all on snakes, and devising methods that may be applicable to them can be difficult and frustrating.

A contemporary experimental test which indicates that animals may have self-discrimination capabilities is the mirror test (Gallup et al., 2002). In this visually oriented procedure, an animal is tested to determine whether it can recognize its own image mirror as itself rather than a conspecific. Typically the mark test is used: An animal that grooms itself would try to remove a visible mark placed on it that could not be seen without using the mirror. Up until now, this test has been successfully passed by some apes and few other animals (Chang et al., 2017; Plotnik et al., 2006; Prior et al., 2008; Reiss & Marino, 2001; Suarez & Gallup, 1981; Walraven et al., 1995), although there are objections to all demonstrations of self-recognition capabilities in nonprimates, mainly on methodological grounds (Gallup & Anderson, 2018, 2019).

Snake brains are about half the size of the brains of equally sized lizards, and they are not considered to be cognitively adept, even among other nonavian reptiles (Font et al., 2023). However, snakes are very vomer-olfactory-oriented animals, and they can be tested for self-discrimination in an “olfactory” modification of the mirror test. This test exploits the fact that other signs may direct the animal to recognition of its own body, such as olfactory cues.

In one application of this test, the males but not the females of individually housed garter snakes (*Thamnophis sirtalis*) raised on different diets were able to discriminate between their own odors and the odors of conspecifics placed on the cage liners, pointing to the possibility of the existence of a “chemical mirror” (Burghardt et al., 2021).

Burghardt et al. extensively discussed the controversy of applying a chemical mirror test to snakes, giving suggestions for future research.

In another study on self-recognition/self-awareness, copperhead ratsnakes (*Coelognathus radiatus*) were tested using a divider with holes to get from the starting point in one arena to another area that contained a shelter. The holes in the divider were of different diameters. Snakes in an experimental group had their body diameter increased by feeding. The snakes in the experimental group showed a reduced number of attempts to use holes of inappropriate diameters for crossing between the arenas compared with the control group, where all holes were appropriate in diameter, suggesting that the snakes may be aware of the limits of their body. The snakes also showed behavioral flexibility by continuing to respond appropriately when the position of holes was randomized (Khvatov et al., 2019). Although there are no snake studies on taking an alternative route to a goal (i.e., detouring), studies of functional morphology/biomechanics suggest that snakes would be able to adjust their routes according to the structural complexity of the environment (Mansfield & Jayne, 2011).

Snakes can also discriminate heterospecifics, and this ability is apparently affected by the complexity of the environment. Corn snakes (*Pantherophis guttatus*) were individually kept in either environmentally enriched or standard enclosures and were subsequently tested for discrimination of familiar versus unfamiliar human odors. The snakes, after being housed in the enriched enclosures, spent significantly more time investigating an unfamiliar human odor, suggesting successful discrimination of the handlers and an attraction to novelty. In contrast, snakes housed in the standard enclosures did not discriminate between the two odors, despite exploring the stimuli for the same amount of time (Nagabaskaran et al., 2021).

Almli and Burghardt (2006) found that prolonged exposure to enriched housing along with live feeding resulted in different behavioral profiles compared with black rat snakes (*Pantherophis obsoletus*) maintained in standard enclosures. This points to the fact that the experiments on captive snakes should be carefully designed, as they may give different results in different captive environments.

Rattlesnakes also possess a chemical sense of self, discriminating between their own scent and the scent of conspecifics (Chiszar et al., 1991). Moreover, if the animals are put in clean cages, they spend more time chemically investigating them and defecate sooner than animals that have been taken out and returned to the cages with familiar odors (Chiszar, Wellborn, et al., 1980; Wellborn et al., 1982).

Quantitative Abilities

Snake studies on quantitative abilities are nonexistent. We do not know whether snakes possess quantitative abilities that are similar to or close to those present in other reptiles. We also do not know whether they can discriminate size and make decisions about it (De Meester & Baeckens, 2021). In a study on prey size discrimination, northern watersnakes (*Nerodia sipedon*) took smaller prey when they had a chance to do so (Andreadis & Burghardt, 2005). However, the prey characteristics that were used in the assessment of its size remain unknown.

Conclusion: Where to Go From This Moment in Time?

We have limited knowledge on both the physiology and cognition of snakes, which opens wide the possibilities for researchers in comparative cognition to fill in the gaps. Next I outline some possible avenues for future research that could help integrate snakes, and potentially other nonstandard study animals, and thereby broaden our understanding of cognition as a whole.

Almost all the predatory events in snakes are essentially the same: detecting the prey (by thermovision, ordinary vision, or chemically) → orientation toward it → predatory strike → subduing the prey (either by venom or body coils) → relocation of prey → finding the prey's head for easier swallowing (snakes do not always swallow prey from the head) → swallowing. In this sequence we see a finely tuned interplay of physiology and behavior to achieve a specific goal: the procurement of food. Such physiological actions to orchestrate behavior are seen in all animals, and snakes are no exception. However, snakes are limbless and elongate, and these conditions put many constraints on them, behavioral ones included. For instance, snakes neither have very movable eyes nor react to the conspecifics in the way the birds and mammals, or even lizards and chelonians, do; at least for the majority of snake taxa. These limitations make studies on gaze-following a difficult task. These constraints plus a low level of sociability can make studies of snake cognition challenging. Are these unfavorable sets of conditions a reality? Yes! Do they imply that snakes are intractable animals concerning cognition studies? No! Twenty-two years of maintaining a large academic snake colony has taught me that one has to observe snakes carefully and know the biology of each species if that person is to be successful in studying snake behavior and cognition. Failure to do this frequently ends with meager data and disappointment (Seigel, 1993). Often, a novel, sometimes unconventional

approach is needed, as well as experimenting with the species one wants to use to see which setup and experimental approach would be the most appropriate. Initial logic tells us to use active, large species, as they have larger heads and brains. However, this notion can be misleading, as many ecological factors drive the evolution of brain size in reptiles (De Meester et al., 2019). The key is in matching of the right question with the right approach with the right species. In my experience, even the most intractable species can be used if right approach can be devised. Critical anthropomorphism may help in the process (Burghardt, 1985, 1991). The most obvious place to start cognitive research with snakes is to study species with a long research history. Rattlesnakes are a typical example. Communal hibernation, birth-giving, and maternal attendance in rattlesnakes has been known for decades, perhaps even centuries, both anecdotally and scientifically. Carefully watching rattlesnakes near their dens will reveal various forms of intraspecific communication. The snakes frequently lie coiled, with bodies in close contact, sometimes intertwined, suggesting that they do some form of tactile, perhaps even visual, communication. However, currently we can only speculate about this, as up until now there have been no studies on communication other than chemical near or in communal hibernacula or rookeries. Someone who is keen on studying rattlesnake biology and cognition may find this a fertile area for future research. Just as kin sociality in rattlesnakes was determined using molecular biology methods (Clark et al., 2012) and the actions, quite unexpectedly for the snakes, pointing to higher cognitive processes were determined by filming (Putman & Clark, 2015), the “cryptic” cognitive processes in rattlesnakes may be revealed by putative new or correctly applied old methods (e.g., possible video monitoring inside and in the vicinity of den). All that is needed is interest leading to informed research on the topic.

Besides communication, social cognition in snakes is virtually unknown. However, observations such as paternal defence of females and young by a male timber rattlesnake (*Crotalus horridus*) mentioned in the section on cognitive abilities forms an excellent starting point for the study of snake social cognition. This behavior clearly points to a sophisticated cognitive process that could be on the level of that of primates: In the given ecological situation, the male is probably aware of the impending danger (approaching humans) and his relation with the nearby conspecifics (female and young) and applied the appropriate action (defensive threat behavior). We do not know the frequency of such behavior in the wild, but even one observation of such an act makes it clear that

dismissing snakes as un sentient animals is premature at best, if not simply false.

Other examples of social behavior are equally impressive: the observation that Cuban boas (*Chilabothrus angulifer*) hunt bats cooperatively in cave passages in such way that they take into account the other snakes' position at the cave entrance and, by doing this, form a fence that increases their hunting efficiency by blocking the flight path of the bats (Dinets, 2017). Cuban boas could also be an excellent choice for the study of snake social cognition.

Many other areas, including those covered here, such as spatial cognition and self-recognition, are still in their infancy when it comes to the study of snakes. Especially ripe for study might be the study of quantitative abilities where, as just reviewed, virtually nothing is known.

Further investigations into the cognitive abilities of snake also need to be supported by a better understanding of their perceptual systems. Much ground is to be covered there as well. For example, physiological studies of snake eyes tell us that snakes are well equipped with the cells that enable them to see at least some colors (see the section "Vision '*sensu stricto*'"). However, we know nothing of the real color perception and its importance in snake behavioral ecology.

Sometimes, even casual observation of captive snakes can reveal "unusual" behaviors: In my snake colony, I unexpectedly observed a captive male saharan sand viper (*Cerastes cerastes*) piling up sand under the heat lamp in a cage in the spring after hibernation. After the heap was approximately twice (i.e., about 20 cm) as high as the sand level in the rest of the cage, it buried itself in it and stayed there for about 3 hours. When the sand was not piled, the temperature under the heat lamp was around 33 °C. Only one male did this and only during spring; females, even when gravid, never showed such behavior. This individual snake did this for 7 years, every spring, during his residence in the colony. This unusual behavior suggests that snakes have behavioral flexibility and the ability for invention like many other species, and this warrants further investigation.

A need for the future, which indeed could become a flourishing area of cognitive science, is a research link between the nervous system and cognition—some kind of cognitive neuroethology. For years, comparative cognition studies have not been able to link mental processes in animals to the function of specific parts of the brain or the other nervous system parts. Perhaps a second generation of molecular biology techniques may take a step toward this understanding. Snakes may be especially relevant in this endeavor because of their different physiology from

many other species. Genomes of several snakes have been sequenced, and an entire web page is devoted to snake genomics (<https://www.snakegenomics.org/>). The genome of the Burmese python (*Python bivittatus*) shows characters indicative of the extreme anatomy and physiology (Castoe et al., 2013). However, the published linkage (or at least the attempts of it) of the described genes to specific physiological function and performance is still nonexistent. Although the linking of "omics" data to specific traits can be very difficult, if not controversial (Joyner & Pedersen, 2011), in the future we may be able to see the advances in this area, and this could reflect on our understanding of "brain-endocrine system-cognition" axis.

I must emphasize that the key to success in using snakes as experimental animals is in an integrative approach, in applying modern and unorthodox techniques integrating knowledge from psychology (e.g., cognitive and comparative psychology) and biology (e.g., ethology, behavioural ecology, general herpetology). Just because they are different from other nonavian reptiles (i.e., limbless absolute predators), using snakes in cognitive research may widen our views on how cognition actually manifests itself on different evolutionary levels. As previously mentioned, snakes are not considered to be very cognitively adept (a layman would say "clever" or "smart") animals, compared with other nonavian reptiles. However, cognition is linked to the survival and fitness, and all animals need to be cognitively fit to be able to defend themselves, catch food, and reproduce. Snakes still exist in various biotopes, sometimes in substantial numbers, being restricted to move farther into the polar regions only by their ectothermy. Because they have existed on Earth much longer than humans, they surely must have the cognitive capacities needed to survive. I speculate that snake cognition may manifest itself in a different way than that of avian reptiles (birds) and mammals, which may be challenging to quantify. To what extent and how, we still do not know. This information, obtained from studying snakes, may help us to get a more generalized view on cognition that is broadly applicable across the animal kingdom rather than mainly restricted to birds and mammals.

My opinion is that snakes should also be studied because they are fascinating animals by themselves, not only because they are good research models in some areas of biology and psychology. Simple research could be done by citizen science methods, and such observations might be very useful. Snakes are often kept as pets, and some snake keepers are experts in maintaining them in captivity. Many keep rare or unusual species about which we know very little. Getting the right information from such species

could be invaluable for our understanding of snake biology and, especially, cognition. Although citizen science concerning snakes has mainly been done in the area of field conservation (Goiran & Shine, 2019; Santos et al., 2022; Todd et al., 2017), there is no reason why it couldn't be done with captive animals. If snake keepers can be instructed how to acquire specific data on their animals, they may obtain useful information on many aspects of snake behavior and cognition. I wrote this review in the hope that it will entice the interest of psychologists (but also of biologists) in snakes as experimental animals and to encourage those working with standard animals (e.g., rats, primates, birds) in comparative research to consider animals that are especially different in their traits, such as snakes, as a rich source of interesting information in the cognitive sciences.

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