

## **Evidence for sentience in reptiles**

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## Summary

Though we cannot directly assess consciousness in non-human animals, an increasing number of researchers are adopting the *marker approach* – amassing evidence of behaviors that may indicate consciousness to determine which species are likely to be conscious. Here, I review the evidence for behavioral markers of sentience (also called phenomenal consciousness) in reptiles, a historically understudied class. Reptiles show some evidence of experiencing pain, stress, and pleasure, demonstrate active sleep and open-ended associative learning, display complex social cognition, and appear capable of self-recognition. However, in all these areas, the behaviors considered key indicators of sentience have often not been tested. There is a need for much more research on all these behaviors and their mechanisms in a wider range of reptile species.

## Introduction

Students of comparative psychology have avoided discussing consciousness in non-human animals, even as the study of other cognitive processes has flourished (Shettleworth, 2010a). The reason for this is not, I believe, our lack of direct access to consciousness, as this is equally true of all cognition. Rather, the key distinction is that most cognitive processes can be defined functionally, allowing us to identify behavioral markers that can be used to report on the presence or absence of those processes. If the cognitive process called memory involves the creation and use of representations of environmental features, then an animal will be able to use a representation of some features of a maze, for example, to solve that maze faster on repeated exposure to it. The behavior of the animal, appropriately tested, can definitively indicate the presence or absence of a particular type of functionally specified cognition.

Unfortunately, there is no consensus on what consciousness is for, even in humans (Ludwig, 2022). This has made it difficult for comparative psychologists to identify appropriate behavioral markers. Since we don't know what consciousness contributes to cognition, it is possible to construct, for any behavior, a convincing "killjoy" explanation (Dennett 1983; Shettleworth, 2010b) that does not rely on consciousness as a mechanism.

Progress in studying animal consciousness must therefore rely on a different methodology than the one we use for other forms of cognition. Here, I adopt the *marker* approach (Birch, 2020), focusing on behaviors that might, under some reasonable theory of consciousness, serve as evidence for its existence (Burghardt, 1985, reviews the history of this approach). The strength of the marker approach is enhanced by assembling a wide range of possible markers: if an animal displays many behaviors that might require or be facilitated by consciousness, then we should be more likely to believe that the best explanation for those behaviors includes consciousness as an intervening variable. This approach is congruent with Birch's *facilitation hypothesis* (Birch, 2020), and is closely aligned with the recent New York Declaration on Animal Consciousness (Andrews et al., 2024).

There are many different types of consciousness. Some, like the internal monologue that language-capable humans have, are *a priori* unlikely in most animals and would be almost impossible to identify from (non-verbal) behavioral markers. Here, I focus on the simplest form of conscious awareness, sometimes called sentience or phenomenal consciousness: the ability to have an internal, possibly valenced, mental experience or feeling (Block, 1995; Browning & Birch, 2020).

There is much debate on which behaviors might serve as good markers for non-human sentience. Some have suggested selecting behaviors that are always accompanied by conscious awareness in humans (Mason & Lavery, 2022) or focusing on specific kinds of learning (Ginsburg & Jablonka, 2021). The paucity of research in most areas of reptile cognition serves as an additional restriction on the criteria that can be considered – we simply have no information on whether, for example, any reptile can acquire cross-modal associations (Birch, 2020). In light of this, I present evidence on a wide range of potential markers, including behaviors that have been used to support attributions of sentience in other taxa (such as the presence of active sleep; Tononi, Boly & Cirelli, 2024), that only occur in the presence of consciousness in humans (like complex associative learning; Mason & Lavery, 2022), that have been taken to indicate more sophisticated forms of consciousness (like self-recognition; McFarland, 2009), as well as indicators of states such as pain or pleasure. I also discuss social complexity, for reasons discussed below. I exclude markers for which there is no reptilian evidence (positive or negative). For example, though judgment bias tests are considered excellent markers of affect, no demonstrations of

the paradigm exist in any reptile, as far as I am aware (Bethell, 2015). Wherever possible, I present both behavioral and neurophysiological evidence for each marker.

All current approaches to animal consciousness, perhaps unavoidably, assume that it will look a lot like human consciousness. Whether in our choice of behavioral markers, the neuroanatomy we think is indicative of sentience, or the types of internal experience we posit, our approach is always anthropocentric. However, it is unlikely that consciousness in other animals is identical to ours. A central tenet of comparative psychology is that animals evolve those cognitive skills that improve their fitness, suggesting that cognition should vary in a systematic way with ecology (Vonk & Shackelford, 2012). Even if sentience originated in the distant past, it will have subsequently been shaped in different ways by the different selective pressures operating on different species (Nagel, 1974). Reptiles – mostly carnivorous ectotherms that have scales and perceive their world primarily via odor – inhabit very different environments from ourselves, and we should expect their sentience (if they are sentient) to be correspondingly different from ours.

Figure 1 presents a simplified phylogeny of the amniotes (the group of animals that includes reptiles, birds, and mammals). As the figure makes clear, birds are reptiles (Modesto & Anderson, 2004): an alligator is more closely related to a chicken than either of them is to a snake, for example. This means that, to the extent that phylogenetic arguments provide good evidence for cognitive abilities, data on bird behavior are relevant to the consideration of reptile sentience. If we accept that birds and mammals are likely sentient (Low et al., 2012), then either sentience evolved at least twice or it is ancestral to all amniotes, including reptiles (or it is ancestral to amniotes but was independently lost in the several non-avian reptilian lineages).

Figure 1 additionally demonstrates how ancient the reptilian class is. Snakes and lizards, for example, diverged from each other at around the same time as eutherians (such as humans) diverged from monotremes (such as the duck-billed platypus). Crocodylians and turtles (and birds) split from the rest of the reptiles about 100 million years before that. Thus, the various reptile groups have been evolving apart from each other, in an incredibly diverse range of habitats, for a very long time. This should make us wary of drawing broad conclusions about sentience in the entire class based on existing research on a small number of species. Much more work is required to fill in these gaps in our knowledge.

## **Markers of sentience in reptiles**

### *Indicators of pain*

Pain is the canonical valenced internal experience and the one most often discussed, possibly because animals' ability to suffer has far-reaching moral implications (Shevlin, 2020; De Waal & Andrews, 2022). As a result, behavioral markers of pain have been identified, including motivational trade-offs, guarding of injured body parts, preferring or self-administering analgesics, and learning how and where to avoid painful stimuli (Sneddon et al., 2014; Crump et al., 2022). Though there are anecdotal reports from veterinarians and zookeepers attesting that they can feel pain (Ayers, 2016), there is surprisingly little controlled empirical work on reptile pain, and there are no demonstrations of any of these markers in any reptile (as far as I know).

For example, I am aware of only one study demonstrating motivational trade-offs in a reptile, though not involving pain: green iguanas (*Iguana iguana*) will leave a warm shelter in order to obtain a

preferred food at a colder location (Balasko & Cabanac, 1998). Iguanas will also inhibit their reactions to potentially painful stimuli when observed (by a human), possibly due to stress-induced immobility (Fleming & Robertson 2012). A similar effect is observed in rats exposed to cat odor (Lester & Fanselow 1985).

Research veterinarians, attempting to identify effective analgesics for use in reptiles, have tested several species on their responses to presumably painful stimuli, and how various analgesics affect those responses. Much of this research has been conducted using the Hargreaves test (Hargreaves et al., 1988), adopted without modification from mammalian pain research. In this test, a beam of intense IR light is focused on an animal's limb or other body-part, rapidly heating it, and the animal's latency to withdraw from the stimulus is measured. In mammals, analgesics reliably increase the maximal heat an animal will tolerate (e.g., Foley, Liang and Chrichlow, 2011). There is some controversy around using a heat-based test in ectotherms, who may have fewer or more unevenly distributed receptors for heat than mammals (Mosley, 2011), but the test continues to be used because it appears to work. Other analgesic tests have measured reactions to other nociceptive stimuli (electrical stimulation, capsaicin or formalin injections), post-operative behavioral changes (James et al., 2017; Kinney, Johnson and Sladky, 2011), or physiological measures (such as heart rate), with largely congruent results. Some researchers may have induced analgesia by cooling reptiles when attempting to anesthetize them for surgery (e.g., Greenberg, 1977).

Using these methods, a variety of substances that function as analgesics in mammals have been tested on reptiles, yielding – to date – a confusing and inconsistent picture. For example, many effective analgesics operate by stimulating the opioid system, and most vertebrates share several classes of opioid receptor. Mu-opioid receptor agonists, such as morphine or fentanyl, appear to have analgesic effects in turtles (*red-eared sliders*: Sladky, Miletic and Paul-Murphy, 2007, Kinney et al., 2011, Baker, Sladky and Johnson, 2011, Mans et al., 2012, Sladky, Kinney and Johnson, 2009; *Speke's hinge-backed tortoise*: Wambugu et al., 2010), crocodiles (Kanui & Hole, 1992) and lizards (*bearded dragons*: Sladky, Kinney and Johnson, 2008, Couture et al., 2017; *tegus*: Leal et al., 2017; *green iguanas*: Greenacre et al., 2006; *anoles*: Mauk et al., 1981), but not snakes (*corn snakes*: Sladky et al., 2008; *ball pythons*: Kharbush et al., 2017). However, Kappa-opioid receptor agonists do not appear to decrease pain in turtles (*red-eared sliders*: Sladky et al., 2007, 2009) or lizards (*bearded dragons*: Sladky et al., 2008; *green iguanas*: Fleming & Robertson, 2006 [but see Greenacre et al., 2006]; *tegus*: Leal et al., 2017) but may work in snakes (positive evidence in *corn snakes*: Sladky et al., 2008; negative evidence in *ball pythons*: Olesen et al., 2008). Both alpha2-adrenoceptor agonists and antagonists increase pain tolerance in turtles (*Speke's hinge-backed tortoise*: Makau et al., 2016; *marsh terrapin*: Makau et al., 2014), snakes (*ball pythons*: Bunke, Sladky and Johnson, 2018, Karkus, Sladky and Johnson, 2021) and lizards (*tegus*: Bisetto, Melo and Carregaro, 2018). Non-steroidal anti-inflammatory drugs (NSAIDs) appear to have no effect on pain in ball pythons (Olesen et al., 2008).

The preceding paragraph represents, as far as I can tell, the entirety of the empirical literature on analgesia in reptiles. A total of 10 species are represented (4 lizards, 3 turtles, 2 snakes, 1 crocodylian), in a class that contains in excess of 10,000. As much of this research has been conducted for the benefit of veterinary practice, little is known about the mechanisms that underlie these effects. The wide variation in responses may result from anatomical differences (e.g., in receptor densities; Mosley, 2011), differing behavioral tendencies in the expression of pain, or physiological differences in, for example, sedative effects of the drugs (Perry and Nevarez, 2018). It is also worth noting that none of these results

demonstrate seeking or self-administering of analgesics, nor do the paradigms used test for learning about painful stimuli. In other words, none of the data at hand speak to the criteria philosophers have identified as good markers for the experience of pain. The best we can say is that reptiles display nociception (McKune et al., 2015).

### *Indicators of stress*

Pain is not the only form of negative affect, and there is some evidence for stress or anxiety in reptiles (reviewed by Gangloff and Greenberg, 2023). Being handled or restrained appears to be stress-inducing for reptiles, as evidenced by increased corticosterone levels in bearded dragons (*Pogona vitticeps*; Stockley, Wilkinson and Burman, 2020), green iguanas (Kalliokoski et al., 2012), tree lizards (*Urosaurus ornatus*; Moore, Thompson and Marler, 1991), ball pythons (Kreger & Mench, 1993), Western diamond-backed rattlesnakes (*Crotalus atrox*; Schuett et al., 2004), alligators (*Alligator mississippiensis*; Lance & Lauren, 1984), and Kemp's Ridley sea turtles (*Lepidochelys kempii*; Gregory & Schmid, 2001), but not in green anoles (*Anolis carolinensis*; Borgmans et al., 2021) or blue-tongued skinks (*Tiliqua scincoides*; Kreger & Mench, 1993). High housing densities, which may be stressful, also increase corticosterone levels in some female side-blotched lizards (*Uta stansburiana*; Comendant et al., 2003) and alligators (Eley et al., 1990). Iguanas increase their heart rate when handled (Cabanac & Cabanac, 2000) and both dwarf tegus (*Callopistes maculatus*; Cabanac & Gosselin, 1993) and wood turtles (*Clemmys insculpta*; Cabanac & Bernieri, 2000) display an "emotional fever" – increasing their internal temperature by preferring a warmer location – after being handled (an effect also observed in rodents and humans; Briese & deQuijada, 1970).

Red-footed tortoises (*Geochelone carbonaria*), but not bearded dragons, habituate more slowly to novel than familiar environments, presumably because the former are stressful (Moszuti, Wilkinson and Burman, 2017). Brown wall-lizards (*Podarcis liolepis*) provided with conspecific-scented pieces of paper decrease their escape behaviors, perhaps as a result of decreased anxiety (Londoño et al., 2018). Male green anoles show many behavioral signatures of stress, including changes in body color that correlate with corticosterone levels (Greenberg, 2002). Reactions to environmental enrichment, reviewed in the next section, may also expose stress or anxiety responses induced by deprivation.

These data paint a more cohesive picture than the work on pain and analgesia reviewed above, and strongly suggest that reptiles can experience of stress, even displaying hormonal profiles very similar to those seen in stressed mammals (Gangloff and Greenberg, 2023).

### *Indicators of pleasure*

In addition to pain, sentient animals might also have the capacity for positively valenced feelings, like pleasure or contentment. There is far less research on this topic, but some reptiles display behaviors that might reflect positive affect in their responses to enrichment. Reptiles will often show a preference for an object, conspecific, or environment, and these may serve as indicators of motivation (to choose) or desire (Kirkden and Pajor, 2006). Some reptiles exhibit play, which has been considered a good marker for positive affect or "joy" (Nelson et al., 2023).

The effects of physical enrichment – providing animals stimulating environments that allow for performing natural behaviors (Young, 2013) – have been tested in several reptiles. Corn snakes (*Pantherophis guttatus*; Hoehfurner et al., 2021a) and Western hognose snakes (*Heterodon nasicus*;

Nagabaskaran, Skinner and Miller, 2022) show a preference for enriched over barren enclosures when given a choice. Corn snakes prefer a larger cage in which they can fully stretch out over a smaller one (Hoehfurtner et al., 2021b). Galapagos turtles (*Chelonoidis nigra*) choose specific enrichments over others (Mehrkam & Dorey, 2014) and Eastern box turtles (*Terrapene carolina*) prefer enriched environments and show a decrease in stress-related behaviors and physiology when housed in one (Case, Lewbart and Doerr, 2005). However, providing climbing enrichment to the semi-arboreal Eastern fence lizard (*Sceloporus undulatus*) appears to have no effect on either behavioral or physiological measures of stress (Rosier and Langkilde, 2011), and increasing cage size or structural complexity has no effect on behavior or physiology in green anoles (Borgmans et al., 2018, 2019). Housing under enriched conditions also improves some aspects of cognition in ratsnakes (*Elaphe obsoleta*; Almlil & Burghardt, 2006) and corn snakes (Nagabaskaran et al., 2021) and, in western hognose snakes, living under enriched conditions increases brain size (Nagabaskaran et al., under review), an effect also seen in other taxa (Diamond, 2001).

Leopard geckos (*Eublepharis macularius*) engage with some enrichment items added to their cages more than expected by chance, and this increases the diversity of behaviors they display – a possible mark of positive affect – but has no effect on the incidence of abnormal repetitive behaviors (which may themselves be indicative of negative affect; Bashaw et al., 2016). Repetitive behaviors also decrease in turtles offered enrichment objects (Therrien et al., 2007).

Several reptile species have been shown to engage in play – performing non-functional behaviors with objects or conspecifics (Burghardt, 2005; Dinets, 2023). Nile softshell turtles (*Trionyx triunguis*) play with objects floating in the water and this reduces repetitive and self-injurious behavior (Burghardt, Ward and Rosscoe, 1996). Sea turtles (*Chelonia mydas*) have also been observed playing with floating objects (Mann & Mellgren, 1998). Several studies have observed play behaviors with objects and with humans in monitor lizards (*Varanid spp.*; Burghardt et al., 2002; Khandakar et al., 2020), including repeatedly shredding and then scattering leaves without consuming them (Kane, Davis and Michaels, 2019). American alligators (Lazell & Spitzer, 1977) and Cuvier's dwarf caimans (*Paleosuchus palpebrosus*; Heinbuch & Wiegman, 2000) have both been observed playing with and in falling water.

Though these examples are suggestive, the essence of play ensures that such reports remain anecdotal and investigations of the motivations underlying the behaviors are almost never undertaken (though this is also true of studies on play in mammals). Nonetheless, the presence of play-like behaviors in reptiles, demonstrating a preference for certain objects or activities over others, along with their preferences for specific (enriched) environments, suggest that they are capable of wanting things (Browning & Veit, 2023) and may experience joy (Nelson et al., 2023).

### *Sleep*

Most animals spend significant portions of their lives asleep (Miyazaki, Liu and Hayashi, 2017). In mammals and birds, sleep occurs in two distinct forms: slow-wave and active (also called paradoxical or rapid eye movement [REM]), which are distinguished on the basis of both behavioral and neurophysiological characteristics. Importantly, it has been suggested that active sleep is a conscious state, at least in humans (Chow et al., 2013).

Sleep is defined behaviorally as a state of immobility during which animals are less responsive to external stimuli (Siegel, 2008). Slow-wave sleep is characterized by reduced EEG frequency and activity,

especially in the brainstem. During active sleep, however, EEG activity is similar to waking, and is accompanied by distinct behavioral effects like loss of muscle tone and rapid movements of the eyes (Siegel, 2008). Though definitions of sleep (both behavioral and physiological) have been criticized as mammal-centric (Libourel & Herrel, 2015), reptiles from many groups display states seemingly analogous to slow-wave sleep (see Ayala-Guerrero & Mexicano, 2008).

Several reptile species exhibit two different phases of sleep, and some of them show eye movements during one of those phases (reviewed in Libourel & Herrel, 2015). However, the EEG patterns that accompany this phase of sleep vary across reptiles and, in many cases, are nothing like those observed in mammals and birds (Flanigan, Wilcox & Rechtschaffen, 1973; Libourel & Barrillot, 2020). For example, eye movements during sleep have been recorded in turtles and lizards, but often in the absence of changes in EEG patterns that match mammalian REM sleep (Libourel & Herrel, 2015). Alternation between states similar to both phases of mammalian sleep has been observed in bearded dragons (Shein-Idelson et al., 2016). A similar alternation of states has been seen in tegus (*Salvator merianae*), though the exact EEG patterns differ from those seen in any other species (Libourel et al., 2018). Administering fluoxetine, a serotonin reuptake inhibitor, decreases the duration of active sleep in tegus, an effect also observed in mammals (Libourel et al., 2018). Many reptile species display large amplitude spikes in their EEG during sleep, which do not correspond well to any mammalian or avian sleep stage (Flanigan, Wilcox & Rechtschaffen, 1973).

The complications in attributing mammalian-like active sleep, a putatively conscious state, to reptiles are primarily due to its being defined based on both behavioral and neurophysiological factors. Reptilian brains are structured differently from mammalian or avian brains and their EEG patterns are correspondingly different, presumably even when performing the same function (there are ongoing debates about the function of active sleep, even in mammals; Siegel, 2011). For example, bearded dragons alternate between the two phases of sleep they show with a clock-like regularity unheard of in mammals or birds (Shein-Idelson et al., 2016). Some studies of turtles have failed to find differences in EEG between waking and sleeping states altogether, and many reptiles fail to show an increase in sleep duration after being sleep-deprived (Libourel & Herrel, 2015; but see Flanigan, Wilcox & Rechtschaffen, 1973). These variations likely result from ecological differences within reptiles and between them and mammals, in ways that we have not yet started to unravel. Nonetheless, at least some reptiles display two phases of sleep with differing EEG signatures, and exhibit eye movements during one of them, suggesting they experience a state analogous to mammalian REM.

### *Learning*

One commonly cited marker for sentience is the capacity for 'complex' learning. For example, Ginsburg and Jablonka (2021) propose that sentience emerged with the evolution of Unlimited Associative Learning, a term they use to refer to learning that is open-ended and supports associating compound or novel stimuli, second-order associations, trace conditioning (in which there is a temporal gap between the two events to be associated), and rapid reversal (Birch, Ginsburg and Jablonka, 2020). It has also been suggested that instrumental conditioning entails consciousness, at least in humans (Skora et al., 2021). Unfortunately, as for other markers, there is little research on these kinds of complex learning in reptiles, though there is a large and growing literature on their general ability to learn (Szabo, Noble and Whiting, 2021).



Many reptile species show associative learning, both classical and instrumental, including associating novel cues such as colored discs or arms of a maze with various rewards (reviewed in Burghardt, 1977, Wilkinson and Huber, 2012, and Szabo et al., 2021). However, none of these experiments employed a trace conditioning preparation (i.e., in all cases, the conditioned stimulus was still present when the unconditioned stimulus began), with the possible exception of a taste aversion experiment on eastern gartersnakes (*Thamnophis sirtalis*; Burghardt, Wilcoxon and Czaplicki, 1973). Many of these conditioning experiments included assessing reversal learning, when the formerly correct and incorrect choices are reversed. It has been suggested that improvements in the speed of learning such reversals is indicative of sentience (Birch, 2020). Many learning studies in reptiles only reverse the reward contingencies once, precluding an analysis of this effect, but there are a few exceptions (reviewed in Burghardt, 1977). Species that have been found to improve over successive reversals of a spatial learning task include Painted turtles (*Chrysemys picta*; Kirk & Bitterman, 1963; Holmes & Bitterman, 1966), spectacled caimans (*Caiman crocodilus*; Williams, 1968), American alligators and crocodiles (*Crocodylus acutus*; Gossette & Hombach, 1969), green iguanas (Alkov & Crawford, 1966), red-footed tortoises (Bridgeman & Tattersall, 2019), monitor lizards (Gaalema, 2011), and banded geckos (*Coleonyx variegatus*; Kirkish, Fobes and Richardson, 1979).

No study that I am aware of has examined cross-modal learning (combining cues from more than one modality to learn an association) in any reptile. However, plains gartersnakes (*Thamnophis radix*) more strongly avoid a prey type previously paired with illness based on its odor when it is presented using brightly colored forceps, suggesting that the visual stimulus increases the salience of the odor (Terrick, Mumme and Burghardt, 1995).

I am not aware of any serial reversal study in which a reptile did not improve over successive reversals, but there is a small number of such studies overall. Other than reversal learning, despite a large literature on basic learning in many species of reptile, there is limited evidence – positive or negative – for any of the other kinds of learning that, in mammals and birds, are sometimes taken as markers of sentience (Birch, 2020; Birch, Ginsburg and Jablonka, 2020; Mason and Lavery, 2022).

### *Social complexity*

Though social behavior is not usually considered a behavioral marker for sentience, managing social complexity may be an important driver of the evolution of intelligence (Dunbar, 1998) and establishing and maintaining social structures may require simple forms of theory of mind. Social learning – learning about the environment by observing the choices of others – requires the kinds of complex associative skills often considered indicative of sentience (see above). In contrast to most other behavioral markers for sentience, there is a large and detailed body of literature on social structures across a wide range of reptile species, despite reptiles having been considered asocial for many years (Doody, Burghardt and Dinets, 2013). A comprehensive review of all the many ways reptiles engage in social living has recently been published (Doody, Dinets and Burghardt, 2021), and I will only highlight a few examples that emphasize the sophistication reptile social behavior can attain.

Many reptiles come together at specific times of the year for mating, hibernating, or egg-laying, and can form complex social networks. Eastern gartersnakes prefer to aggregate with specific other individuals in their group (at least in the lab; Skinner & Miller, 2020), a preference that solidifies as they age (Skinner & Miller, 2022), and a similar dynamic appears to occur in Otago skinks (*Oligosoma otagense*; Elangovan et al., 2021). Butler's gartersnakes (*Thamnophis butleri*) form association networks that are

structured by sex and age (Skinner et al., 2023), and timber rattlesnakes (*Crotalus horridus*) aggregate more with kin than with unrelated snakes (Clark et al., 2012). Plains gartersnakes preferentially aggregate with conspecifics that they have not previously competed with for food (Yeager & Burghardt, 1991), and Butler's gartersnakes prefer to aggregate with individuals that are on a different diet from themselves, presumably because this also reduces food competition (Lyman-Henley & Burghardt, 1994). In ball pythons, generally considered a solitary species (though they readily aggregate in the lab; Skinner et al., 2024a), social experiences activate the same network of brain areas as in mammals (Skinner et al., 2024b). These similarities in social behavior and neurophysiology across vertebrate classes suggest an ancient origin of complex sociality, and its underlying cognition.

Sea kraits (*Laticauda semifacitata*) hunt cooperatively and take on different roles in the hunt (Somaweera et al., 2023), and there are reports of Cuban boas (*Chilabothrus angulifer*) spacing themselves across the mouth of a cave to more efficiently capture departing bats (Dinets, 2017). There are also anecdotal reports of cooperative hunting in crocodylians (Dinets, 2014). Some forms of behavioral coordination in reptiles may be driven by vocal communication (reviewed in Lin, Lin and Godfrey, 2024). For example, Nile crocodile (*Crocodylus niloticus*) hatchlings use vocal cues to coordinate their hatching times (Vergne et al., 2007). However, evidence of intentionality is usually required in order to consider communication or coordination as markers of consciousness (Dennett, 1983), and this has not been tested for in any of these cases.

Some reptiles have also been shown to use social information in sophisticated ways. Red-footed tortoises (Wilkinson et al., 2010a), leopard geckos (Simpson & O'Hara, 2019), bearded dragons (Siviter et al., 2017), and alligators (Zeiträg, Reber and Osvath, 2023) all gaze-follow, using the direction of gaze of a conspecific to decide where to direct their attention. Gaze following can be used to identify a general direction in which to look (low-level gaze following) or a specific location to examine (geometric gaze following). The latter of these, but not the former, has been linked to conscious social skills like theory of mind in humans (Kuhn et al., 2018; but see Teufel et al., 2010). Reptiles, however, despite being tested for both forms, have so far only demonstrated low-level gaze following (Siviter et al., 2017; Zeiträg et al., 2023).

Social interactions can also be used to expose other types of cognition. For example, like mammals, rattlesnakes display social buffering – a reduction in stress responses when in the presence of a conspecific – suggesting they can experience stress (Martin et al., 2023). Reptiles also show social learning: Florida red-bellied cooters (*Pseudemys nelsoni*; Davis & Burghardt, 2011), red-footed tortoises (Wilkinson et al., 2010b) and bearded dragons (Kis, Huber and Wilkinson, 2014) can socially learn responses that will lead to a food reward; Australian tree skinks (*Egernia striolata*) learn to move a disk covering a food reward faster if they first observe a trained conspecific solving the task (Whiting et al., 2018), as do Italian wall lizards (*Podarcis sicula*), even if the demonstrator is a lizard of a different species (Damas-Moreira et al., 2018).

Reptiles thus display a wide range of sophisticated social structures (Doody, 2023) and use social information in goal-directed ways. This bolsters evidence that they are capable of complex open-ended learning, experience (socially induced) stress or pleasure, and create and manipulate complex representations of their social environment.

*Self-recognition*

Self-awareness is a form of consciousness, sometimes defined as the ability to become the subject of your own attention (Gallup, 1977). In non-human animals, passing the Mark Test of mirror self-recognition (MSR; Gallup, 1970) has been considered evidence for self-awareness, at least in apes, though there are good reasons to doubt that passing a test of self-recognition entails self-awareness (Heyes, 1994; Brandl, 2016; Freiburger, Miller and Skinner, 2024). The Mark Test consists of marking an animal that has been habituated to the presence of a mirror with a colorful dye somewhere on its body that is not visually accessible except using the mirror. Animals are considered to pass the test if, upon seeing the mark, they reach for their own body, rather than towards the mirror (or to an invisible control mark; Gallup, 1977).

Most reptiles are not primarily visual and tests of self-recognition in reptiles have used an olfactory version of MSR, in which the subject is presented with its own modified odor instead of its own marked image (Horowitz, 2017). Using this test, eastern gartersnakes but not ball pythons have demonstrated self-recognition (Freiburger, Miller and Skinner, 2024). Male gartersnakes (but not females) investigate their own soiled bedding more than that of a same-sex conspecific consuming the same or a different diet (suggesting the discrimination is not purely based on detecting what the stimulus snake has been eating; Burghardt et al., 2021). Blue-tongued skinks investigate paper containing their own odor less than that of a conspecific (Graves & Halpern, 1991), as do several species of *Liolaemus* lizards (Aguilar, Labra and Niemeyer, 2009). Male desert iguanas (*Dipsosaurus dorsalis*) will flick their tongues (a sign of interest) at their own tails more after encountering their own odor than that of a conspecific (Alberts, 1992) and female tokay geckos (*Gekko gecko*) tongue-flick at the ground of their home enclosure – saturated with their own odor – more when presented with the odor of a conspecific than their own odor (Szabo & Ringler, 2023).

In the only attempt I know of to test self-awareness independently of self-recognition in a reptile, ratsnakes were shown to learn to avoid attempting to move between compartments via an opening that was too small for them to fit through, and would even avoid larger openings when they had recently eaten (and were therefore larger; Khvatov, Sokolov and Kharitonov, 2019).

Self-awareness is often considered a more complex conscious state than sentience, but is assumed to require or be built on sentience (Mason and Lavery, 2022). Though the debate over whether passing tests of self-recognition entails self-awareness continues (Gallup and Platek, 2023), reptiles have passed these tests at rates similar to birds.

## **Conclusion**

Though it is not possible to directly address questions about consciousness in the same way as other cognitive processes, indirect methods such as the marker approach offer a way to estimate the likelihood that a species is conscious. This approach has recently been used to argue that a wide range of species, including all vertebrates and many invertebrates have “at least a realistic possibility” of being sentient (Andrews et al., 2024). The value of such evidence lies primarily in its ability to encourage more research into animal sentience and the mechanisms of complex behaviors (Miller, 2024). Reptiles have long been neglected in psychological research and have often been considered cognitively simple (Burghardt, 1977). As a result, there is very little empirical evidence on which to judge claims about their sentience. In many cases, specific criteria proposed as behavioral tests of a conscious state, like those for pain (Crump et al., 2022), have simply never been tested in any reptile.

In many cases, reptile behaviors appear structured similarly to those of mammals – for example in how they learn (Szabo et al., 2021), interact socially (Skinner & Miller, 2020), or show stress (Greenberg, 2002). Though there is very little neurophysiological data, what there is appears to follow the same trend, with representations of social interactions (Skinner et al., 2024) and changes in brain waves across sleep states (Shein-Idelson et al., 2015) partly matching those seen in mammals. This strongly suggests that these behaviors and brain organizations are ancient in origin and conserved across all amniotes. If these behaviors in mammals can serve as evidence for sentience (Low et al., 2012), then they should elicit the same commitments when observed in reptiles.

However, if reptiles are sentient, their sentience is fundamentally different from ours in many respects (as argued more generally by Nagel, 1974). Reptile brains are structured differently from ours, and reptile ecology varies widely both within the class and between reptiles and mammals (Font, Burghardt and Leal, 2023). These differences will certainly have shaped reptile sentience in ways that diverge from how mammalian evolutionary history has shaped ours. Reptiles do not appear to have REM sleep in the same way mammals and birds do; they may not experience pain – and relief from pain – in the same ways we do; they likely interpret social cues, such as gaze direction, differently; and their self-awareness will not function in the same way as ours. Only by conducting more research into the mechanisms of all these behaviors, in a wider array of species, can we begin to understand whether there is anything it is like to be a reptile and explore the full diversity of ways sentience can manifest.

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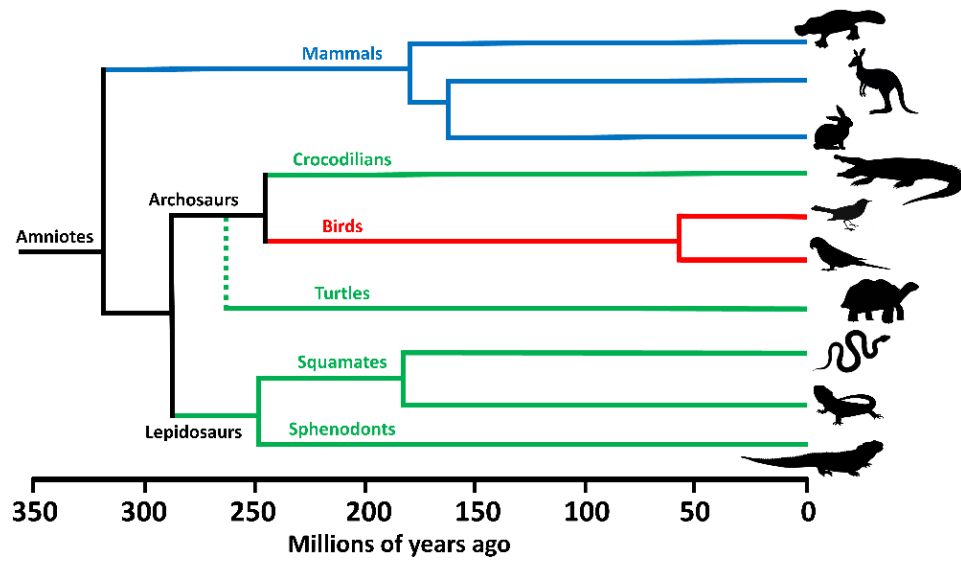
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**Figure 1.** Simplified phylogeny of extant amniotes, with a focus on reptiles. Reptiles are shown in green, mammals in blue, and birds in red. The turtle lineage is disputed. Phylogenetic data are from *TimeTree* (Kumar et al., 2022).