Reptiles: Misunderstood, maligned and mistreated

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For centuries, researchers and non-specialists alike have dismissed the behaviour and cognitive abilities of reptiles as simple and moronic compared to those of other vertebrates. This widespread misconception can be traced, at least in part, to long-standing fallacies regarding reptilian brain size and organization. Until recently, the brains of reptiles were thought to be small and lacking the neural structures that underpin complex cognition in birds and mammals. In reality, reptile brains are not as small as previously thought and possess the same major subdivisions found in all vertebrates. Furthermore, a growing body of research shows that the brains of reptiles support a rich behavioural repertoire and sophisticated cognitive abilities on par with those of mammals and birds. Thus, the persistent myth of the sluggish, primitive, uninteresting reptile is based on prejudice, ignorance, and multiple misunderstandings, is utterly inconsistent with the available evidence, and should be abandoned.

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What makes humans different from other animals has been a long-standing concern and a source of endless debates. Where some consider that an impassable chasm – the Cartesian abyss – sets us apart from the rest of the natural world, others – following Darwin – see only a small crack in the ground, quantitative rather than qualitative differences. Theoretical arguments and empirical evidence notwithstanding, many still believe that humans are a pinnacle of some sort, superior to and essentially different from other animals – a view sometimes described as 'humaniqueness' (Pepperberg, 2008) or human evolutionary exceptionalism (McCullough, 2015). Those in the exceptionalist camp often point to the existence of presumably unique human traits, such as language, consciousness and, most important, our (vastly overrated) intelligence. But it is becoming increasingly difficult to be an exceptionalist – at least a rational one. It is true that we do things that other animals cannot do, but

the reverse is also true. Each animal species is unique and different from any other, otherwise zoologists would not assign them to different species. Diversity is the predictable outcome of the evolutionary process. We should expect to find differences, but also commonalities arising from patterns of shared ancestry and adaptation to similar environmental conditions. This applies as much to morphology or physiology as it does to behaviour and cognition (Shettleworth, 2010). Obtaining convincing evidence for cognitive commonalities between humans and nonhumans was important for early defenders of Darwinism, but initially much of that evidence was anecdotal. Recently, however, a growing literature is revealing behavioural and cognitive accomplishments in all kinds of animals that were once thought to be our species's exclusive domain. Rats laugh when they play or are tickled, and demonstrate empathy towards a trapped cage mate; dogs show evidence of referential understanding; bumble bees play rolling wooden balls and are capable of social learning and complex problem solving; roosters and cleaner fish recognize themselves in a mirror; octopuses use tools. Given this evidence, it is unsurprising that, in April 2024, scientists attending a conference in New York, USA, signed a declaration stating that there is a realistic possibility of consciousness in all vertebrate animals and in many invertebrates (https://sites.google.com/nyu.edu/nydeclaration/declaration).

The available evidence makes it clear that non-human animals are more like us than we used to give them credit for. But there is at least one exception: reptiles. The human–animal gap may be shrinking for some groups, but reptiles apparently do not follow suit. As far as their behaviour and cognitive abilities are concerned, most people blithely assume that reptiles are, compared to other animals, below par. Although admitted as possibly conscious by the signatories of the New York declaration, reptiles are often portrayed as primitive, instinct-driven, slow-witted and lacking even the most basic intellectual abilities. In fact, for a long time the motivation of many studies of reptile behaviour was to characterize the primitive or primordial state from which the more complex behaviour of birds and mammals evolved. Even fish, despite their undeserved reputation for bad memory, often rate better than reptiles (Nakajima *et al.*, 2002). Catchy titles such as "The evolutionary advantages of being stupid" (Robin, 1973), referring to turtles, or "Reptiles are the real bird brains" (Fessl, 2022), certainly do not help to dispel the widespread notion of reptiles as the cognitive morons of the vertebrate radiation. Perceptions of reptiles have consequences for the way we treat them and cater for their welfare in captivity (Burghardt, 2013), and may also hinder conservation efforts, as detailed in a book that inspired the title of this essay (Warwick, 1990).

What did reptiles do to deserve such a bad reputation? Negative attitudes towards reptiles in part stem from the fact that they are perceived as potentially dangerous to humans. Crocodiles, large lizards like Komodo dragons, and large constricting snakes are feared as potential man-eaters. Venomous snakes evoke intense fear (Landova *et al.*, 2020), although the risk of envenomation is often overestimated. Of approximately 4,100 species of

snakes on the planet, only 600 are venomous, and only 200 (less than five per cent) can kill or cause serious damage to a human. In the USA, a country with no shortage of venomous snakes, deaths by snakebite average five per year (National Institute for Occupational Safety and Health, 2024), less than one tenth of those caused by dog attacks (National Center for Health Statistics, 2023). Another factor contributing to the negative public image of reptiles is that most people perceive them as relatively alien life forms. We are more likely to empathize with animals that are similar to us in behaviour and physiology (Prato-Previde *et al.*, 2022). But many reptiles have reduced legs or lack them entirely. Others spend all their lives encased in a protective shell. As ectotherms, they spend long periods of time basking in the sun (although in this they resemble many tourists on the Mediterranean coasts). Depending on their body temperature they can have a sluggish demeanour, or they can move at lightning speed (don't try to outrun a croc!). They are covered in hairless, scaly skin, they lack facial expressions, and they rely on mysterious sensory modalities such as infrared/ultraviolet vision and vomerolfaction.

But arguably the main enemies of reptiles are ignorance and prejudice. With more than 12,000 recognized species, they are the second largest vertebrate group after fish. However, research on vertebrate behaviour and cognition is heavily biased in favour of mammals and birds. Many researchers, lured by the appeal of working with 'higher vertebrates' and improved funding opportunities have eschewed the study of groups such as reptiles or amphibians. As a result, we know very little about the behaviour and cognitive abilities of most reptile species. Traditionally, what little research has been done on reptile cognition has focused on turtles, while other groups (lizards, snakes, crocodiles) have received much less attention. But reptiles are an extremely diverse lot, comprising a tremendous range of body forms, behaviours and life-history patterns, which should cast a shadow of doubt on broad generalizations based on work on a limited number of species. Added to this is the fact that our perception of reptile behaviour and cognition is clouded by multiple misconceptions. Recently, I and my colleagues Gordon Burghardt and Manuel Leal devoted a chapter in an edited volume to debunking several myths about reptile behaviour (Font *et al.*, 2023). We focused on seven widespread misconceptions, although many more undoubtedly exist. Our goal was not to assert that reptiles should have the same privileged status as birds or mammals in the pantheon of comparative cognition. Reptiles resemble birds and mammals in many ways, but they are also very different from them. That is what makes their study so interesting. Instead, our goal was to review an already abundant literature that challenges the traditional view of reptiles as simple, moronic and uninteresting creatures.

Several persistent myths about reptilian behaviour and cognition can be traced, at least in part, to long-standing misconceptions about reptilian brain size and organization. The reptilian brain has often been stereotyped as small, simple and lacking a cerebral cortex – a characterization that is incorrect and based on outdated evidence. Research on reptilian neuroanatomy experienced its heyday in the 1970s and 1980s but has languished over the last few decades.

Thus, compared to the great volume of work on mammalian and avian brains, relatively little is known about the reptilian brain, and studies several decades old claiming that reptiles have small and incomplete brains are still cited as if they were authoritative. It is true that the brains of reptiles are smaller than those of mammals or birds of similar body size, but the difference has traditionally been exaggerated. Many textbooks and review papers report that the bird brain is ten times larger than that of a reptile of similar body size. However, the ten-fold figure is based on a handful of species, small sample sizes (a single individual for most species) and flawed analytical methods. Recent analyses using an expanded dataset and modern phylogenetic comparative methods that allow more precise examination of relative brain size in reptiles show that the actual value is 6.5-fold. A comparison using brain volume and body volume instead of mass to account for reduced body density of birds (an adaptation for flying) further reduces the average difference in relative brain size between birds and reptiles to 5.4-fold (Font *et al.*, 2019).

For decades, we have been hearing stories about the walnut-sized brains of large dinosaurs like *Stegosaurus* or *Diplodocus*. Our own brains, for comparison, weigh approximately 1,350 grams, which is 1,000 grams heavier than the brain of a five-ton *Tyrannosaurus rex* (Balanoff *et al.*, 2013). Indeed, one (apparently serious) hypothesis about the extinction of dinosaurs did not mention asteroids or massive volcanic eruptions, but instead attributed their demise to their "dwindling brain and consequent stupidity" (Benton, 1990). However, across all vertebrates, whether living or extinct, there is a well-documented trend for relative brain size to decrease as body size increases. This trend (technically known as negative allometry) is responsible for large animals having proportionally smaller brains than small animals. So, applying the necessary corrections to account for several flaws in previous estimates of both brain and body size, the large dinosaurs had brains the size that we should expect for a reptile or a bird of their gigantic body size, no more and no less (Hopson, 1977). These brains were responsible for an elaborate behavioural repertoire, including territoriality, dominance hierarchies, male–male combat and courtship behaviour, sophisticated vocal and visual communication, intensive parental care of the eggs and young, gregariousness, cooperative breeding and food-getting behaviour, even play (Rothschild, 2014). It is telling that, although this is often described as an 'avian level' of behavioural complexity, all these behaviours have been documented in non-avian living reptiles, including crocodiles, alligators, caimans and their kin, the dinosaurs' closest relatives among living reptiles (Kramer and Burghardt, 1998; Schuett *et al.*, 2016; Whiting and While, 2017; Doody *et al.*, 2021).

In any case, the extent to which brain size is an indicator of behavioural and cognitive complexity is highly controversial. One might intuitively think that large brains should be found in more intelligent animals, but things ain't quite that simple. Elephant brains are larger than human brains, yet most people would agree that we are more intelligent than the average elephant. The fact that elephants are large animals suggests that the ratio brain-size:body-size may be a better measure of brainpower, but it turns out that many small

animals, such as pocket mice and harvest mice, have relative brain sizes considerably larger than humans and elephants (Striedter, 2005). Recent work has suggested that the number of neurons in all or selected parts of the brain, or patterns of connectivity in neural networks, may be better measures of cognitive ability in a comparative context (Herculano-Houzel, 2017; Barron and Mourmourakis, 2024). But despite some success in correlating brain size or neuron number with ecological, life-history and cognitive variables, the relationship tends to be very noisy (Healy and Rowe, 2007). Also, the correlations become weaker, not stronger, as the taxonomic diversity of sampled groups increases (Barron and Mourmourakis, 2024).

Another widespread misconception holds that the reptilian brain is essentially a mammalian brain that is missing some parts. This idea originated with the work of neuroscientist Paul D. MacLean. MacLean, with precious assistance from astronomer and science communicator Carl Sagan, popularized the triune brain model of brain evolution, that holds that vertebrate brains evolve through the addition of successive layers. According to this hypothesis, reptiles are endowed with only the basic layer, to which two more complex layers were added in the evolutionary transition to mammals first, and then to primates and, of course, humans. To underline the limitations imposed by a brain lacking more evolutionarily advanced layers, MacLean allegedly once pronounced that "it is very difficult to imagine a lonelier and more emotionally empty being than a crocodile". Nothing could be further from the truth. In addition to their own complex emotions, crocodiles seem to be finely attuned to human emotions, according to a recent report (Thévenet *et al.*, 2023). MacLean was a pioneer in efforts to integrate information from evolutionary theory, comparative neuroanatomy and animal behaviour, but his model is clearly at odds with the current understanding of vertebrate brain evolution (e.g. Cesario *et al.*, 2020). The three layers implied by the triune brain were already present in the common ancestor of all living vertebrates and can be found, in modified form, in all its descendants (Emery and Clayton, 2005). Contrary to MacLean's model, reptiles have the same major subdivisions found in a mammalian brain, including an emotional brain and a neocortex (Striedter and Northcutt, 2020; Font *et al.*, 2023). Thus, MacLean's claim about the emotional emptiness of crocodiles and, by extension, other reptiles is untenable on theoretical grounds, as well as being contrary to evidence that reptiles can in fact be quite emotional animals (Cabanac *et al.*, 2009; Lambert *et al.*, 2019; Martin *et al.*, 2023).

A remark often attributed to Mark Twain is that "It's easier to fool people than to convince them that they have been fooled". Mistaken ideas about brain evolution in vertebrates are no exception. Although the triune brain model has been discredited, it continues to have considerable intuitive appeal, and its influence has been subtly perpetuated, even among specialists. Unfortunately, MacLean's ideas about reptilian brain and behaviour set the trend for many years and are still considered cutting edge in some quarters, where the behavioural repertoire of reptiles is thought to be limited to the four Fs: fight, flight, feeding and... reproduction.

However, the notion that reptiles are unsophisticated in their behavioural repertoires is increasingly out of step with reports of complex behaviour in many species. Current work shows that reptilian behaviour is as rich, complex and elaborate as that of many mammals and birds (Gillingham and Clark, 2023). Lizards have become esteemed models for studies in ethology and behavioural ecology and are a key focal group in research on a diversity of topics, including aggression, reproductive strategies, anti-predator behaviour, and communication. One area where recent research is driving a paradigm shift is social behaviour. Although traditionally considered solitary, uncaring and asocial, recent reviews paint a different picture of reptile sociality (Doody *et al.*, 2013, 2021; Whiting and While, 2017). Some reptiles communicate extensively with one another using smells, sounds, colours and movement-based displays such as head bobs, dewlap extensions, foot shakes and tail-twitches. Some have refined and extended parental care, long-term monogamy and family ties spanning generations. Some hunt, feed, court, mate, nest and hatch in groups. Although diversity is understandable in such a large group, 'social reptile' can no longer be considered an oxymoron.

The familiar view of reptiles as stupid and unintelligent also faces a growing list of exceptions. One problem that has vexed researchers working on comparative cognition for decades is confusing our own ignorance for the lack of a particular cognitive trait. One often hears that chimpanzees (or primates, or mammals) are the only animals capable of a given cognitive feat, only to wonder in what other species has the ability been tested. Absence of evidence is not evidence of absence. Many authors have uncritically assumed that the small and allegedly primitive brains of reptiles must condemn them to a life of cognitive mediocrity. The unfortunate consequence of this misperception is that the cognitive abilities of reptiles have rarely been tested. This, in turn, reinforces the notion that sophisticated cognition is absent in this group. However, recent work documents rather complex cognitive achievements in all kinds of reptiles (Leal and Powell, 2012; Wilkinson and Huber, 2012; Font, 2020; Roth *et al.*, 2019; De Meester and Baeckens, 2021). At least some reptiles show fast and flexible learning, long-term memory, spontaneous problem-solving abilities, remarkable navigational abilities, quality and quantity discrimination, gaze following, tool use and social learning. Even self-recognition, which in primates and other mammals is taken as an unequivocal proof of self-awareness, has been demonstrated in some lizards and snakes (Burghardt *et al.*, 2021; Szabo and Ringler, 2023).

Many learning tests conducted with reptiles during the last century failed because they did not take into account peculiarities of their morphology, physiology and behaviour. Temperature at the time of testing, for example, is a crucial variable, as most reptiles will not perform efficiently at temperatures that may be adequate for work with mammals and birds. Studies using test conditions and paradigms more appropriate to reptilian physiology and behaviour clearly demonstrate that turtles, crocodiles, lizards and snakes are capable of performing most traditional learning tasks (Burghardt, 1977a; Szabo *et al.*, 2021; Font *et al.*, 2023). But to reveal the full extent of their learning

abilities requires adopting an ethological approach – that is, to view learning and other forms of cognition not from our perspective, but from the perspective of species' normal behaviour under natural circumstances.

As a token of appreciation for his relentless defence of reptiles and reptilian ethology, I believe it is appropriate to end this essay by quoting Gordon Burghardt: "we need to be on guard against 'science' being uncritically accepted as supporting and encouraging our deeply held prejudices. This paper is but a partial brief in behalf of a maligned and oppressed class" (Burghardt 1977b: 189). His powerful message is as valid today as it was when these words were written almost 50 years ago. It is time we take stock of the prejudices that blind us and take animals in general and reptiles in particular for what they really are: beautiful, fascinating and magnificent creatures.

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A common lizard, Scotland
(Joe Gray)