

Cold-blooded cognition: new directions in reptile cognition

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The field of comparative psychology has traditionally focussed on investigating the cognitive abilities of a small number of mammal and bird species, but in order to understand the evolution of cognition, it is essential to examine cognitive abilities across a large range of vertebrates. Reptiles are particularly interesting in this context as they represent a key amniotic Class that do not develop under high, stable temperatures, which can produce phenotypic variation in the population. As their patterns of development differ substantially from those of birds and mammals reptiles can be used to investigate fundamental questions relating to factors shaping cognition; questions that cannot be asked in mammals and birds. In this review, we highlight some of these areas of interest and consider how the emerging field of reptile cognition can address crucial questions in cognitive science.

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Introduction

In order to understand the evolution of cognition, it is essential to compare abilities across the animal kingdom. Similarities and differences in performance of the same task, alongside studying the structure of the brain, can inform us about evolution of various cognitive abilities. Traditionally, comparative psychology has focussed a lot of attention on a very few species of mammals and birds [1] and although the number and diversity of species studied has been increasing, the bias towards mammals and birds remains [2]. This work has provided strong evidence that similar, potentially complex, cognitive abilities (e.g. tool use) can be shared among distantly

related species [3] whose evolutionary history and brain structures differ substantially [4]. Reptiles are a key Class in developing an understanding of the evolution of cognitive abilities amongst amniotes. The study of similarities and differences in their cognition can inform about homologies and analogies of cognitive mechanisms across the amniotes [5]. Traditionally reptiles are considered to be limited in terms of their cognition [6], however, when tested in physiologically appropriate conditions, they show an impressive suite of cognitive abilities (e.g. [7^{**},8^{**},9–11]).

Reptiles are also interesting in the study of cognition because of their pattern of development. In birds and mammals, development takes place under stable conditions at high temperatures (though other sources of variation may influence the developmental environment (e.g. [12])). In contrast, reptiles develop normally at a range of temperatures, which fluctuate during incubation, and this affects the phenotype of the hatchling in terms of sex, growth rate, physiology, pigmentation, locomotion, and behaviour (for reviews see [13,14]). Therefore, these differing early environments may also be affecting the cognitive abilities of individuals (e.g. [15–18]), which may have long-term fitness implications. The stable environments of avian or mammal development do not produce this range of phenotypic variability.

The study of reptiles is essential for understanding cognitive evolution, but this group also allows us to test fundamental hypotheses in the field of cognition which simply cannot be tested using mammals and birds. This review will summarise some key trends in the field, wherever possible we will present all relevant recent work, therefore, any imbalance in the species discussed is likely to reflect the paucity of knowledge in the area. We will then go on to outline some (but by no means all) areas in which the use of reptiles can change our understanding of the processes shaping cognition before finally discussing some future directions for the field.

The impact of early environment on cognition Effects of incubation temperature

Personality and cognitive performance appear to be linked within a species [19,20]. Therefore, differences in personality are likely to play an important role in understanding individual differences observed in cognitive performance [20,21]. As such, it is essential to consider the impact of early environmental conditions on personality when considering its impact on cognition. Our

recent work assessed the impact of incubation temperature on bearded dragons (*Pogona vitticeps*) in two classic personality tests — behaviour towards a novel object, and behaviour in a novel environment — tests were repeated after a few days and several months [22**]. Although incubation temperature had a short-term effect on the time spent in close proximity to a novel object, no long-term effect was observed [22**]. Hence, variation in incubation temperature within the normal range may impact the development of behavioural traits rather than long-term differences in personality. This in turn may influence cognitive performance over development, which could result in long-term differences in cognitive ability.

Incubation temperature outside the normal range appears to have an even greater effect on the behaviour of offspring. Holleley *et al.* [23] showed that incubation at a very high temperature ($\geq 32^\circ\text{C}$) produced bearded dragons that were genetically male but functionally female. These animals exhibited behavioural traits that appeared to be more male-like than genetic females. This included behaviours associated with personality, for example, higher activity levels and faster emergence from a shelter [24*]. Though the mechanism underlying these differences is unknown, incubation at extreme ends of the temperature range produces offspring that behave in a manner that is different from individuals incubated within the normal temperature range; how this impacts fitness has yet to be studied [24*].

Anatomical differences have been shown in brain structure and neuron density under different incubation conditions; at hatching hot-incubated Eastern three-lined skinks (*Bassiana duperreyi*) have greater neuron density in parts of their medial cortex than their cooler incubated counterparts [15]. This is supported by behavioural data which shows that incubation environment impacts learning, with hot-incubated skinks of the same species performing better in operant learning tasks than cold-incubated individuals [16–18]. In contrast, bearded dragons incubated in cooler conditions perform better in both an operant [25] and a social learning task [26].

These studies suggest that differences in cognition are not based on absolute differences in temperature but are likely to reflect the environment in which the animals are hatching into. Responses to incubation temperature are likely to differ across species and habitat but a hotter incubation environment may result in offspring that are better adapted for survival in that temperature range [22**]. This is contemporary because habitats across the globe are being increasingly affected by environmental change, which creates novel challenges for the animals living there [27]. Reptiles are particularly interesting in this context because of their reliance on external sources of heat [28]. Whilst genetic adaptation can be slow,

changes in behaviour may allow more rapid adaptation to the novel conditions [29]. Cognitive abilities are likely to be important in relation to this as they influence all aspects of decision making [30].

Impact of early social environment

In contrast to mammals and birds, many reptile species provide limited or no parental care of eggs or their offspring [31]. This provides opportunities to control and manipulate the social environment during early stages of development so as to try to disentangle the impacts of social environments on cognition.

Traditionally, social interactions among eggs have been assumed to be limited as each egg is isolated by the shell. Embryonic communication is well known in birds [32] although its effects on subsequent social behaviour are unknown. In reptiles, embryonic communication has recently been reported [33–35] and has been shown to influence behaviour post-hatching [36]. Hatchling water snakes (*Natrix maura*) from eggs incubated in isolation occupied a larger space, were more mobile and maintained less physical contact with conspecifics than counterparts incubated in a clutch where eggs were in contact [36].

The social environment post-hatching also seems to impact behaviour. Veiled chameleons (*Chamaeleo calyptratus*) reared in social isolation after hatching had a longer latency to catch prey, exhibited more submissive behaviour and different colouration from their socially-reared counterparts [37], although this has not yet been shown to impact cognition. In the only study of its kind, Riley *et al.* [38] reared the group living tree skink (*Egernia striolata*) in social isolation or in groups. Contrary to the prediction that those raised in a social environment would perform better in a spatial cognitive task, results revealed that social environment did not have an effect on learning in a biologically relevant spatial task [38]. It remains unknown whether these conditions would impact on performance of a social cognition task.

Impact of early cue experience on spatial learning

Much cognition research with Chelonia has investigated spatial navigation with the focus on the impressive long-range navigational feats of sea turtles [39–41] and short-range spatial learning in terrapins and tortoises [9,42–45]. There is evidence for use of geomagnetic cues, visual cues and response-based strategies in these species [46].

The importance of early life experience on this ability has been examined in the loggerhead turtle (*Caretta caretta*), known to migrate the long distances across the Atlantic Ocean. Geomagnetic cues were manipulated during incubation, by placing magnets around the eggs, and were shown to impact on hatchling navigation. The hatchlings from the manipulated magnetic field swam in random

directions, while the control group oriented towards the migratory route, suggesting that experimental magnetic fields during incubation can alter hatchlings ability to navigate using magnetic cues [47].

Recent field studies on translocated terrapins (*Chrysemys picta*) revealed that individuals under the age of four were able to follow paths of adults [48**] but this ability was lost in older individuals. This suggests that there may be a critical phase for learning. This may be particularly important in the context of changing environments.

Future directions

We have highlighted recent work investigating the impact of early environmental conditions on reptile cognition. Much remains unknown, however, we hope we have demonstrated how the use of reptiles can provide insight into exciting new cognitive questions. Future studies need to involve more species and to fill in the gaps in our understanding. In terms of the traditional comparative approach, three key directions are required, which are discussed below.

Development of model reptile species: Comparative investigations of reptile cognition tend to discuss findings relative to our understanding of similar processes in mammals and birds. However, lack of data prevents an effective and comprehensive comparison. Therefore, we need to systematically replicate classic studies conducted in mammals and birds with reptiles that we feel can be representative model species. One candidate for this would be the red-footed tortoise (*Chelonoidis carbonaria*), a species that has proved adept across a number of cognitive domains [49] including social [10,50,51], visual [7**,52] and spatial cognition [9,42–44].

Cognition across a range of reptile species: Generally, studies examine the cognitive abilities of one or two species and consider it in terms of what reptiles may be capable of. However, this approach would be unacceptable in mammals and birds and simply highlights the lack of knowledge for reptiles. In general, the choice of species used for this work lacks a systematic approach. Studies comparing the cognitive abilities of species selected in a systematic way, on the basis of phylogeny, would prove informative. Further, research on a wider variety of species from all four orders of reptiles would inevitably lead to a better understanding of phylogeny of cognition.

The impact of behavioural ecology on reptile cognition: Much work in comparative cognition uses the behavioural ecology of closely related species to predict differences in cognitive abilities [53]. This approach has proved extremely fruitful and should be harnessed in the field of reptile cognition. Some early research has revealed that feeding ecology impacts reversal but not spatial learning

in congeneric lizards [54]. However, much more work which uses this approach with a wider range of ecological factors and over a greater variety of taxa are required.

Understanding the adaptive value of cognition

To understand the adaptive value of cognition, it is essential to develop biologically appropriate, hypothesis driven tests that can be run in the laboratory or the field. Field experiments will inherently have less control than those in laboratory settings, however, captive work cannot tell us about the selection pressures that operate under natural conditions. It is thus essential to integrate both laboratory and field work to better understanding of mechanisms and adaptation value of reptile cognition. This must be investigated in terms of the adaptive value to the animal, but also the impact that the cognitive processes may have on the ecosystem around it [7**,55].

Conclusion

In order to gain a fuller understanding of the evolution of cognition, it is essential to investigate the cognitive abilities of reptiles. To do this appropriately, we need to: firstly, conduct work with model species that are comparable to the vast amount of research undertaken with mammals and birds; secondly, compare species that are of interest in terms of phylogeny; and thirdly, compare similar species that differ in terms of their behavioural ecology. In addition to fundamental comparative research, the use of reptiles can allow us to test critical hypotheses, such as the impact of early environment on cognitive abilities, in highly controlled environments which are difficult to investigate in mammals and birds. In conclusion, engaging with the study of ‘cold-blooded cognition’ can only be informative and fascinating.

Conflict of interest statement

Nothing declared.

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