## Introduction

Cognition is defined as the processes by which animals gather, preserve, and use information from their environment through perception, learning, memory, and decision making ([Shettleworth 2010](#ref-shettleworth)). These cognitive processes underpin several aspects of animals’ ecology such as foraging, mate choice, antipredatory strategies, and/or social behaviours, that are crucial for the survival and reproduction of animals ([Dukas 2004](#ref-dukas_evolutionary_2004)). Particularly, learning - the acquisition of neuronal representations of new information ([Dukas 2004](#ref-dukas_evolutionary_2004)) - is seen as fundamental for coping with environmental changes by enabling individuals to create new associations between events ([Dukas 2004](#ref-dukas_evolutionary_2004); [Leal and Powell 2012](#ref-leal_behavioural_2012); [Buchanan et al. 2013](#ref-buchanan_condition_2013)). However, the capacity of individuals to acquire new information exhibits natural variation influenced by factors like age, sex, gut microbiota, or the environment where animals develop ([Szuran et al. 1994](#ref-szuran_water_1994); [Lemaire et al. 2000](#ref-lemaire_prenatal_2000); [Zhu et al. 2004](#ref-zhu_prenatal_2004); [Amiel and Shine 2012](#ref-amiel_hotter_2012); [Amiel et al. 2014](#ref-amiel_egg_2014); [Carazo et al. 2014](#ref-carazo_sex_2014); [Noble et al. 2014](#ref-noble_age-dependent_2014); [Alemohammad et al. 2022](#ref-alemohammad_2022_microbiota_learning)). The developmental environment, in particular, plays a pivotal role, as the brain is especially susceptible to environmental influences during early stages of development ([Zhu et al. 2004](#ref-zhu_prenatal_2004)). Hence, investigating the effects of the developmental environment on learning can be essential to understand the evolution of learning and predict animals’ responses towards environmental change.  
In this sense, prenatal Glucocorticoids (GCs) and prenatal thermal environment are known to play a prominent role in shaping learning abilities in different taxa (see [Lemaire et al. 2000](#ref-lemaire_prenatal_2000); [Zhu et al. 2004](#ref-zhu_prenatal_2004); [Amiel and Shine 2012](#ref-amiel_hotter_2012); [Crino et al. 2014a](#ref-crino_corticosterone_2014); [Amiel et al. 2014](#ref-amiel_egg_2014); [Abayarathna and Webb 2020](#ref-abayarathna_effects_2020)). GCs - hormones related to organisms’ response to stress ([Sapolsky et al. 2000](#ref-sapolsky_how_2000)) - exert sustained effects on neural structure and physiology that are associated with animals’ performance on learning tasks ([Lemaire et al. 2000](#ref-lemaire_prenatal_2000); [Zhu et al. 2004](#ref-zhu_prenatal_2004); [Crino et al. 2014b](#ref-crino_corticosterone_2014-learn); [Farrell et al. 2015](#ref-farrell_developmental_2015-learn); [Bebus et al. 2016](#ref-bebus_associative_2016)). Some studies have demonstrated that prenatal stress and high prenatal GC levels impair with learning ([Lemaire et al. 2000](#ref-lemaire_prenatal_2000); [Zhu et al. 2004](#ref-zhu_prenatal_2004); [Farrell et al. 2015](#ref-farrell_developmental_2015-learn)), while others showed diverse effects depending on factors such as sex or the nature of the learning task ([Szuran et al. 1994](#ref-szuran_water_1994); [Crino et al. 2014b](#ref-crino_corticosterone_2014-learn); [Farrell et al. 2015](#ref-farrell_developmental_2015-learn); [Bebus et al. 2016](#ref-bebus_associative_2016)). Similarly, some experiments have shown significant impacts of prenatal temperature on learning in ectotherms ([Amiel and Shine 2012](#ref-amiel_hotter_2012); [Amiel et al. 2014](#ref-amiel_egg_2014); [Dayananda and Webb 2017](#ref-dayananda_incubation_2017); [Abayarathna and Webb 2020](#ref-abayarathna_effects_2020)). For instance, high incubation temperatures have been linked with faster learning rates in skinks ([Amiel and Shine 2012](#ref-amiel_hotter_2012); [Amiel et al. 2014](#ref-amiel_egg_2014)), while velvet geckos incubated at temperatures over their natural range learn slower than those incubated within the natural thermal limits ([Abayarathna and Webb 2020](#ref-abayarathna_effects_2020)). In this vein, the effect of prenatal temperature appears to be linked to alterations in neural structure and metabolic activity ([Coomber et al. 1997](#ref-coomber_independent_1997); [Sakata et al. 2000](#ref-sakata_neural_2000); [Amiel et al. 2017](#ref-amiel_effects_2017); [Beltrán et al. 2021](#ref-beltran_are_2021)) that share some similarities with those resulting from prenatal increased stress or GC levels ([Lemaire et al. 2000](#ref-lemaire_prenatal_2000); [Zhu et al. 2004](#ref-zhu_prenatal_2004); [Du et al. 2009](#ref-du_dynamic_2009)). This suggests that prenatal GCs and temperature can act on the same physiological mechanisms and, thus, both could interact to shape individual variation in learning skills ([Noble et al. 2018](#ref-noble_developmental_2018)). Furthermore, GCs can play an pivotal role in determining vertebrate responses to elevated temperatures ([Crino et al. 2023](#ref-Crino_2023)) potentially fostering natural interactions between temperature and GCs. Despite the proximate similarities of prenatal GCs and temperature effects and the potential role of GCs in vertebrates response to elevated temperatures, our understanding of how these two factors interact remains incomplete.  
In this study, our objective is to explore the interactive effects between prenatal Glucocorticoids (GCs) and the prenatal thermal environment on learning. We utilized two species of skinks, the delicate skink (*Lampropholis delicata*) and the common garden skink (*L. guichenoti*), as model species. We experimentally increased Corticosterone (CORT) - the main GC in birds, reptiles, amphibians, and rodents ([Crino et al. 2023](#ref-Crino_2023)) - levels in the eggs of these two species of skinks and then incubated them at two different temperatures in a 2X2 factorial design. Post-incubation, the juveniles were subjectd to a colour-associative and a reversal task to comprehensively assess their learning abilities. Our hypothesis posits that changes in CORT levels and temperature during early development will induce sustained effects on brain’s morphology and physiology that will ultimately impact learning skills. We predict that individuals exposed to high levels of CORT and/or low temperatures will perform less proficiently in the learning tasks compared to control individuals or those exposed to high temperatures. Additionally, we anticipate that incubation at high temperatures will mitigate the impact of CORT on skink performance, while cold incubation temperatures are expected to enhance the detrimental effects of CORT on learning. We also expect the treatments to affect both tasks equally, with those individuals exposed to high levels of CORT and/or low temperatures performing less proficiently in both tasks compared to control individuals or those exposed to high temperatures. Finally, we expect that the effects of the treatments will be similar in both species, as both species share similar life history traits and are closely related ([Chapple et al. 2011](#ref-chapple_know_2011), [2014](#ref-chapple_biology_2014)), and other cognitive studies have not found any difference between species in learning ([Bezzina et al. 2014](#ref-bezzina2014does)).

## Methods

#### Subjects

*L. guichenoti* and *L. delicata* are small (∼35–55 mm snout-vent length (SVL)), oviparous, and generalist skinks that usually share the same habitat in suburban areas throughout south-eastern Australia ([Chapple et al. 2011](#ref-chapple_know_2011)). Both species have similar breeding periods, but with some differences in reproductive output: while *L. delicata* lays 1 to 6 eggs in only one clutch per season, *L. guichenoti* clutches are smaller (1-5 eggs per clutch) but they usually lay two clutches per season ([Chapple et al. 2011](#ref-chapple_know_2011), [2014](#ref-chapple_biology_2014)). Also, some sudies have found some behavioural divergence between the two skinks ([Chapple et al. 2011](#ref-chapple_know_2011)). *L. delicata* is more exploratory and bolder than *L. guichenoti* ([Chapple et al. 2011](#ref-chapple_know_2011)) which was related to the former’s success as an invassive species ([Chapple et al. 2011](#ref-chapple_know_2011); [Bezzina et al. 2014](#ref-bezzina2014does)), but not with their ability to learn in an associatve learning task ([Bezzina et al. 2014](#ref-bezzina2014does)).

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