The Cold-Blooded Truth About Social Learning

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Abstract

Although it was long believed to be a trait in mammals with higher intelligence, it has been shown that reptiles are also capable of social learning. Because it has been shown that many phenotypical and other behavioural traits are influenced by incubation temperature, this study looked at the role of incubation temperature on social learning in bearded dragons. Two groups of animals, one incubated in hot and one in cold temperatures within the natural incubation temperature range of the species, were given a social learning task and scored on their performance. The results showed that the cold incubated group was significantly faster at completing the social learning task compared to the hot incubated group. This indicates that incubation temperature indeed influences social learning abilities in bearded dragons.

Introduction

It was long believed that social learning was a trait unique to human beings, mainly because social learning can involve various complex cognitive processes such as requiring not only the remembering of a specific action, but also to know when the skill is to be used based on the situation such as in imitation[1]. However research has shown that the act of social learning is present in a wide variety of mammals[2, 3] and birds[4]. Learning through observation from conspecifics in a group can be used in many aspects such as where to forage for food, what mate to choose and acquiring novel behaviour patterns[5]. For a long time the majority of work on social learning continued to concentrate on mammals and birds, while little was known in other orders such as reptiles.

Stimulus and local enhancement

Imitation consists of multiple forms of learning specific actions or information from a conspecific or other animal[6]. The less complex forms of social learning mechanisms, such as local enhancement and stimulus enhancement are simpler mechanisms where information is learned from another animal. In stimulus enhancement an observer's attention is drawn to a demonstrator and to a certain stimulus to provoke interaction with it. For example blue tits in Great Britain in the 1920's and 1930's opened milk bottles tops to get to the cream by performing foraging behaviours such as pecking and tearing. Conspecifics noticed both the birds and the open bottles, which led to the behaviour spreading within the population[7, 8]. This was not imitation because no novel action was learned - the birds' attention was merely drawn to the lid of the bottles - but a form of stimulus enhancement where they learned about which object to interact with. Local enhancement is when the attention of an observer is drawn to a certain location, for example rats have a preference to search for food in locations where fresh rat excrement can be found because it familiarises them with novel food which is most likely safe to consume[9]. It has also been found that it is not necessary for a demonstrator to be present for local or stimulus enhancement, as seen in foraging behaviour in rats where the excrement of a conspecific is enough to provoke local enhancement[9]. Having the demonstrator or a conspecific present may instead lead to social facilitation, another mechanism of social learning where the observer may perform better or worse depending on the situation due to the presence of another conspecific[10]. The most complex form of social learning is imitation, also known as intentional or true imitation, because of the control which is required to reproduce an action[11, 12]. It differs from for example emulation, through which only the results of the action are learned about and not the underlying actions[13]. Imitation is difficult to test because of the amount of factors that influence the results such as social facilitation. Also when interpreting the behaviour it is hard to discern between intentional imitation and copying certain elements of the demonstrator's actions as seen in the other social learning mechanisms. In addition, individual learning could interfere with the experiment if too many trials are given to the subject during which the subject then relies on trial-and-error, and not social learning.

From the 21st century onward reptiles also became a focus group for cognition and behaviour studies and there is evidence of several cognitive behaviours in reptiles such as spatial[14-16] and visual cognition[17, 18], the acquisition of novel behaviour[19] and social cognition[20, 21]. One of the most studied cognitive processes in reptiles is spatial learning, which showed that reptiles, in particular the chelonian, are able to navigate in mazes using spatial cognition[5]. There have been several findings over the past years concerning various reptile species from the chelonian, but also other orders. When looking at social cognitive processes it has been found that the red-footed tortoise (*Chelonoidis carbonaria*), is capable of gaze following, the ability of an animal to match the direction of its line of sight to that of another animal, which was previously only thought to exist in humans and non-human primates[20]. Also the red-footed tortoise has been found to be capable of learning from a conspecific in a detour task, where the animal was placed outside a V shaped fence with a preferred food placed in the centre for them to navigate towards. This showed that even a naturally solitary species can have a social learning capacity[21]. Other reptile species have shown to be capable of behavioural flexibility, the adaptation of behaviour to evolve novel responses to unfamiliar stimuli or alteration of existing behaviour to familiar stimuli, a trait previously thought to be present in mammals and birds only. These were thought to be the only species with the need to adapt their foraging behaviour to food source changes[22]. However research with the tropical lizard *Anolis evermanni* showed that they were capable of not only adapting to changes in food source, but were able to learn to solve novel motor tasks as well as reversal learning and associative learning[22]. When monitor lizards (*Varanus albigularis albigularis*) were tested on their ability to learn how to open a feeding tube they were presented with in three trials, they showed significant improvement in latency after retrieving the first prey, and needed fewer unnecessary tries before opening the tube correctly after the first trial[23]. This showed an ability for individual learning which made Manrod (2008) conclude that studying the cognitive abilities of the squamate reptiles would be a wise next step. Considering the previously mentioned studies focussing on the cognitive process of social learning in the bearded dragon, a reptile from the squamata order may further expand the knowledge of reptile cognition.

Kis and colleagues (2014) found that bearded dragons (*Pogona vitticeps*) were able to learn a specific skill by watching and imitating a demonstrator. The demonstrator was taught the skill of opening a horizontally sliding door to access a reward (mealworm) on the other side. The demonstrator was filmed and the videos were shown to two groups, while the control group received a video of a passive demonstrator. Results showed that the group which had been able to watch and imitate the demonstrator learned to open the sliding door, while none of the control group did[1]. This research shows that reptiles are capable of social learning by imitation and use this to acquire access to a reward. One aim in studying cognitive processes such as social learning is finding what influences the variation between individuals and their ability to practice social learning.

Role of Incubation Temperature

The earliest stages of an animal's phenotypic development are mostly shaped by its environment, with the strongest effects seen in species that develop outside of the mother[24]. Previous studies on egg incubation temperature in reptiles have mainly focussed on morphological differences[25-27], which were shown to occur both in laboratory settings and natural environments[28] suggesting there is a need for phenotypic plasticity in both conditions. However, there has also been research considering cognitive development and function in animals, especially reptiles, and the effect incubation temperature may have in the development. The keelback snake (*Tropidonophis mairii*) was tested on a number of traits, both morphological and physiological, and it was found that many of the traits examined were affected by incubation temperature, with the 'best' results such as faster, longer swimmers and larger offspring coming from the cold incubated group[29]. A recent article described the effect of incubation temperature on brain size of the scincid lizard, and its relation to subsequent differences in cognitive and learning abilities[30]. There it was shown that lower incubation temperatures induced larger telencephalons and larger neurons in the medial cortices, but the neural density was higher in the hot-incubated group. A higher neural density implicates more potential synaptic connections, which is thought to correlate with higher intelligence[30]. This was concurrent with previous learning ability differences seen in experiments with the *Bassiana duperreyi*[30]. If incubation temperature can influence brain size, what other cognitive effects can be found? One aspect of cognition which may be influenced by incubation temperature is social learning. Because incubation temperature affects morphological traits, which have been shown to coincide with traits such as boldness, meaning the willingness of an individual to take risks in a novel situation, and physical capabilities[31, 32], it is not unthinkable that the incubation temperature of reptile eggs may affect the development of social learning in offspring. Only recently have studies also looked at the effect on behavioural traits and learning capabilities in reptiles[24, 31, 33]. The scincid lizard (*Bassiana duperreyi*) has been used in various morphological and social learning experiments[24, 28]. In one such study it is suggested that the scincid lizard (*Bassiana duperreyi*) incubated at a higher temperature performed a spatial learning task better than those incubated at a lower temperature[24, 28]. However, their task was confounded by activity levels which could have resulted in those that moved more were considered faster learners, if latency until starting and speed of moving through the maze was not taken into account.

Why use bearded dragons (*Pogona vitticeps*) for social learning experiments in reptiles?

Because the chelonian order, consisting of tortoises, turtles and terrapins, has barely changed in the past 225 million years it has been the most popular to use for cognitive studies[5]. It contains easy to handle, food motivated species which makes working with them preferable. However the bearded dragon (*Pogona vitticeps*) from the squamata order is also relatively simple to keep and has a calm nature when held in captivity, making it a popular pet as well[34]. Breeding with bearded dragons is simple, as the eggs can be removed from the female after laying and can be incubated at appropriate temperatures according to experimental needs. Also, the hatchlings can be used for experiments within days after hatching[34]. Generally, the bearded dragon is omnivorous with their diet consisting of both greens and insects. They have been found to be easily food motivated, just as animals from the chelonian order, which makes designing experiments easier. Another advantage is that they do not grow to be more than 51 cm (females) to 60 cm (males)[35] and are therefore simple to use in experimental conditions, requiring reasonably sized arenas.

Does egg incubation temperature of bearded dragons (*Pogona vitticeps*) effect cognition?

A study by Amiel et al. (2016) has recently shown how environmental factors drive brain development and the subsequent impact it may have on cognitive skills. Therefore this study looked at the social learning differences between two groups of bearded dragons that were incubated at two different temperatures within their natural range, creating a “hot” incubated group and a “cold” incubated group. Looking at previous research it has been found that the direction of the effect of incubation temperature varies between species[32, 36]. The outcome of the experiment is therefore hard to predict, as either the “hot” or “cold” group may have developed better social learning skills. In previous studies with bearded dragons “hot” incubated animals have been found to be heavier initially, but “cold” incubated animals grew faster and became heavier after hatching[32]. The “hot” animals were also found to be better at foraging and were more active [32]. Most of the previous research on the effect of egg incubation on morphological and physiological traits looks at the effect on hatchlings[24, 26, 27, 31, 33], whereas this study will look at the long term effects of egg incubation temperature in adult bearded dragons (*Pogona vitticeps*) two years after hatching.

Aim of the study

This study will investigate the relationship between environmental temperature during incubation and cognitive ability in adult bearded dragons (*Pogona vitticeps*) when incubated at different temperatures within their natural range. The objective of the study will be to experimentally test the link between egg incubation temperature and social learning using a similar experimental setup that was used to demonstrate social learning in this species[1]. Because of slight differences between the door in the demonstrator video and the door in the test apparatus it is unlikely that any imitation will occur. The experiment will look at differences between two different incubation temperatures, and not social learning from a demonstrator, therefore these differences are considered negligible.

Also the reason for a possible difference between the two groups will be investigated by observing the time spent solving the task and amount of motivation to solve the task. Motivation will be measured as the amount of interactions with the test-door, assessing how motivated each individual is to reach the reward. If motivation is considered equal, the reason for a difference in ability will most likely be caused by the effect of egg incubation temperature. By conducting cognitive studies on animals incubated at different temperatures it is possible, for the first time, to determine how the changes impact on an animal's cognition and behaviour in the long term.

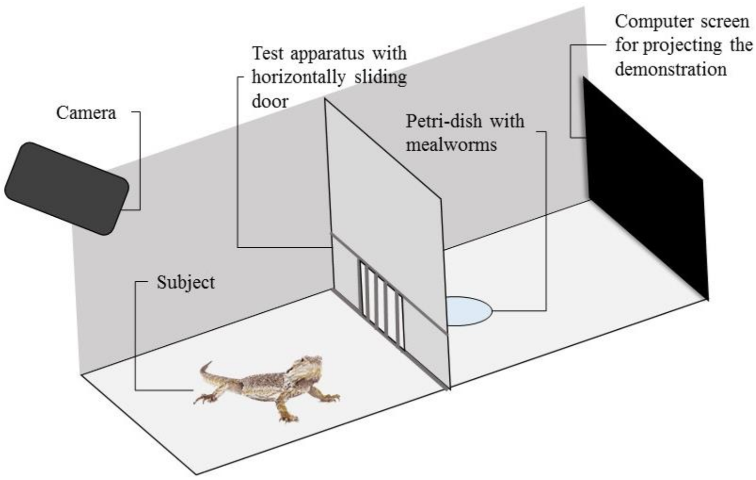
Materials and methods

Subjects

The test subjects were the 13 available central bearded dragons (*Pogona vitticeps*), which were raised at the University of Lincoln and housed in pairs wherever possible. The bedding in the vivarium was newspapers, and each vivarium had a shelter, a water bath and one or two large branches as enrichment.Also heat lamps and UV-light was fitted in each vivarium. The animals were randomly assigned to one of two temperatures as eggs, “cold” 27 ± 3°C and “hot” 30 ± 3°C. “Cold” (n = 6 animals with 3 males and 3 females) were hatched between May 30th and June 1st, and “hot” (n = 7 animals with 4 males and 3 females) were hatched between July 1st and July 8th 2014. All individuals received daily handling, and had taken part in previous behavioural studies, but none involving social learning. The demonstrator used was the same video of a three year old female previously used in the experiment by Kis et al. (2014).

Experimental arrangement

The experimental arena (120 cm x 41.5 cm x 51 cm) had the test apparatus dividing the arena into two equal parts; the test area (where the subjects were located) and the demonstration area (where the computer screen was located). The test apparatus was a wooden board (41.5 cm x 51 cm) placed in the middle of the arena, with a horizontally sliding door with vertical bars in front of the hole (12 cm x 12 cm) in the centre which could be opened to either the left or the right side. The demonstration area had a monitor showing the demonstrator. The glass sides of the arena were covered with white paper, and the floor was lined with newspaper. All testing was recorded with a digital camera (Panasonic HC-V100) on a tripod above the arena.



Procedure

Habituation: all animals were habituated to the arena before the onset of the experiment. A habituation trial started by placing the animal into the arena which contained two Petri dishes with a mealworm (later used as reward in the experiments) at each end. The lizards were given two trials of ten minutes for two consecutive days to explore the arena. The lizards were considered fully habituated when they explored the arena and ate the mealworms. If the animal failed to eat the mealworms within the ten minutes, the habituation procedure was repeated until the lizard met the criterion.

Experimental procedure: the lizards received up to two trials per day for 6 days, with a total of ten trials per animal. At the onset of each trial the lizard was placed in the empty arena for 30 seconds. They then watched the demonstration video (11 s) in which they observed a demonstrator opening a horizontally sliding door to either the left or the right side, using a specific head movement. If the lizard moved away from the demonstration area prior to watching the video, the lizard was placed in front of the screen again before starting the video. The video was mirrored to present the subjects with either rightward or leftward opening, making the video identical for all subjects. Each lizard was assigned either the left or right version of the video. Which version the lizards were assigned was pseudorandomised for both the "cold" and the "hot" groups.

The subject was then moved to the test area and placed behind a screen while the test apparatus was put into place (~15 s). The subject then had five minutes to open the sliding door to access the reward (mealworm). The full trial was recorded. The trial was terminated when the subject successfully opened the door and ate the reward or when the five minutes were over. If the door was opened but the mealworm was not eaten within five minutes the subject received no reward. After each trial the subject was returned to its vivarium. The experimental arrangement was approved by the Ethics Committee within the Faculty of Lincoln University.

Behaviour coding

Absolute success was considered as opening and going through the door to eat the reward, and was recorded as "opening and going through" whereas opening the door but not going through was recorded as "opened". Which side the subjects open the door to was coded either "left" or "right" and "demonstrated side" and "non-demonstrated side". If the subject opened to both sides in the same trial both right and left was coded, and the final side was used to code demonstrated or non-demonstrated side. An opening was defined as a visible gap at either side of the door.

The time taken before a successful opening was measured, where opening was defined again as a visible gap at either side of the door, as well as latency before attempting to open the door, where latency ended when the subject first moved to make contact with the door. The time after latency was recorded as "time trying to open". Also the amount of trials before the first successful opening was recorded, and the amount of successful trials in total.

Motivation was recorded as the amount of head interactions with the door, added with the amount of claw interactions. The total was recorded as a measure for motivation in each trial to separate between a higher success rate due to incubation temperature and due to higher motivation.

Data analysis

The Mann Whitney U test was used for all statistical calculations in SPSS Statistics 24 due to the nature of the data. All figures show average of each incubation group's results ± the standard error of the mean.

Results

Task performance

In the successful trials, where the animal went through and ate the mealworm, the time it took to open the door was significantly lower for the cold incubated group than the hot incubated group (*Mann Whitney U test, P = 0.031*) (see figure 1). For the statistical analysis the animals that only partially or did not complete the social learning task the time was arbitrarily set at 5 minutes (300 seconds) which was the end of the observation time.

There was no significant difference between the cold incubated group and the hot incubated group in terms of opening the test-door *(Mann Whitney U test, P = 0.128*) , although there seemed to be a trend towards the cold incubated group opening the door and going through to eat the reward more often within the trial time (*Mann Whitney U test, P = 0.096*) (see figure 2 a and b). There was also a lot of individual variation in amount of successful trials (table 1) with some animals having no successful openings to some exclusively opening the door every trial. The first successful trial varied from trial 1 to trial 3, with the exception of the animals with no successful trials at all.

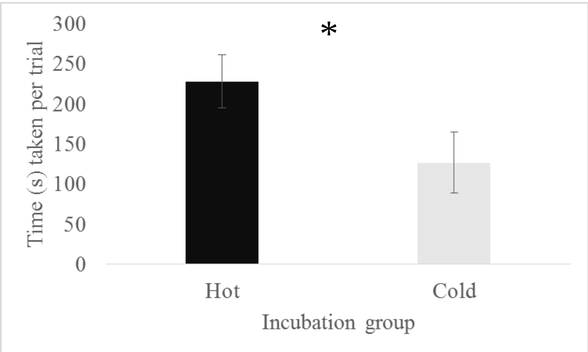


Figure 1

Fig. 1: The average time it took each group to open the door and retrieve the reward (mealworm). Partially completed and unsuccessful trials were arbitrarily set at 300s. **P* = 0.031

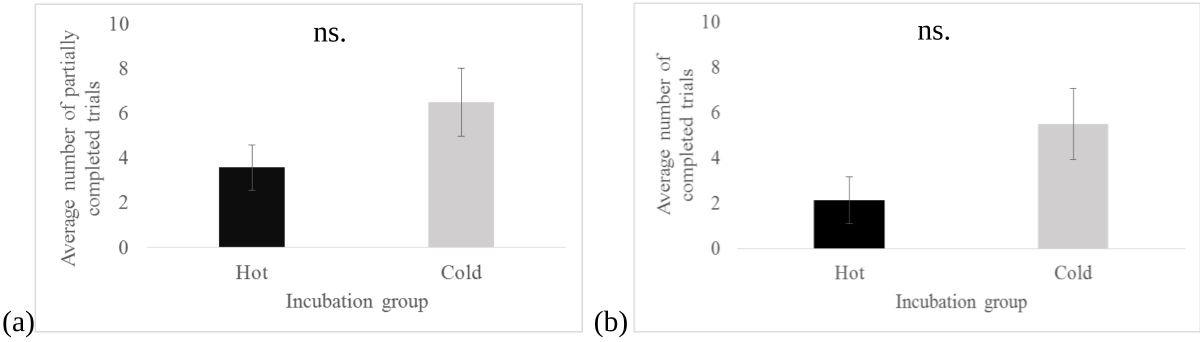


Figure 2

Door opening. (a) The average amount of times the hot and cold group partially performed the social learning task during the trials, *ns*. (b) The average amount of times the full social learning task was completed, i.e. the lizard went through the test-door, and ate the reward (mealworm) for each incubation group. Data shows average ± the standard error of the mean, *ns*.

Animal	Gender	Group	Trial 1	Trial 2	Trial 3	Trial 4	Trial 5	Trial 6	Trial 7	Trial 8	Trial 9	Trial 10
Baron	M	Hot	T	O								
Dragonite	M	Hot	T		O	O						
Grisu	F	Hot	T				T	T	T	T	T	T
Jaime	M	Hot		T	O		O	T		T	T	T
Rodriguez	F	Hot		O	O					O		T
Samira	M	Hot										
Seraphina	F	Hot	O									
Peaches	F	Cold	T	T	T	T	T	O	T	T	T	T
Bowie	M	Cold	T	O	T							
Denny	F	Cold	T		T	T	T		T	T	T	T
Frankie	M	Cold										
Maple	F	Cold			O							
McGee	M	Cold	T	T	T	T	T	T	O	T	T	T

Table 1

Individual trials where (T) is a successful trial where the animal opened the door, went through and ate the mealworm, and (O) is a trial where the animal opened the door but did not go through. In trials (T) the timer was stopped when the animal ate the first of two mealworms in the Petri-dish.

Motivation

Both the head and the claws were used to interact with the door and these were added together to calculate the total amount of interactions. There was barely a difference between the two groups in amount of times contact was made with the sliding door during the trial (*Mann Whitney U test, P = 0.153*).

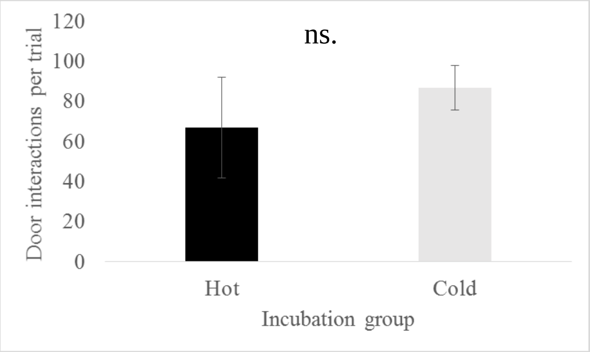


Figure 3

Fig. 3: Motivation to open the door was counted as the average amount of head and claw interactions with the door, *ns*.

Discussion

This study investigated the difference in social learning abilities between two groups of bearded dragons incubated in either "hot" or "cold" temperatures. This was investigated by assessing their ability to learn how to open a test-door to access a reward: a mealworm. The results show that incubation temperature has an effect on social learning, in that the animals incubated at colder temperatures perform better on the social learning task. This is evidenced by the significant time difference between the "hot" and the "cold" groups, where the cold group was significantly faster at solving the task. Also, the difference in successful openings and successful opening and going through the test-door during the entire observation period showed a trend towards the cold group being more successful than the hot incubated group. This difference was not obtained through a difference in motivation, which was evidenced by similar amounts of head- and claw-movements used by each group, indicating that the reason for solving the task faster was indeed the cognitive difference caused by the incubation temperature, and not from the difference in motivation during the trials. Previous research had shown that this group of bearded dragons (*Pogona vitticeps*), when incubated in hotter temperatures, were faster runners and better at foraging behaviour[32]. This study however shows that incubation temperature affects certain traits differently within species, because here the cold-incubated animals were significantly faster learners than the hot-incubated subjects, whereas the hot group was significantly larger after hatching for example[32].

In previous studies with other reptiles it was shown that there is a difference in size and in behaviours such as foraging and running abilities shortly after hatching when varying the incubation temperatures[26-29, 31, 32]. In an earlier study with these bearded dragons, the animals from the hot incubated group were significantly larger and better foragers after hatching, whereas here the cold incubated group has been shown to be better at social learning[32]. This could for example indicate that the cold incubated animals invest more time in observation and learning to be more effective in foraging. This needs to be further investigated before any conclusions can be drawn, however it can be said that incubation temperature affects different traits and abilities differently both within and between species. Other studies such as one by Amiel et. al. (2016) showed that a higher neural density concurred with a better performance in spatial learning tasks in the hot incubated group of the scincid lizard (Bassiana duperreyi) [30]. This is the opposite of what has been found in the bearded dragons, where it was the cold group that showed a higher learning skill than the hot group. Therefore it can be assumed that not all reptiles are affected equally by incubation temperature. A future study could investigate differences in the neural densities in the brains of bearded dragons compared to the findings in the scincid lizard.

The animals in this study are assumed to have been using either stimulus or local enhancement behaviour to solve the task of opening the test-door. By watching the demonstrator, the test animals' attention was drawn to the task of opening the test-door, after which the animals seemed predominantly to use trial and error to reach the same result as the demonstration. A difference that was seen compared to the previous study from 2014 was the inconsequence of performing the task to the demonstrated side[1]. This can be explained by how the subject's attention was drawn to the door which needed to be opened, but not to which side the demonstrator used, thereby encouraging stimulus enhancement. Most subjects were consistent during all ten trials, suggesting that opening and collecting the reward (mealworm) reinforced the same side to be opened in the following trials, though this was not always the case. Still, individual learning could also be considered as a part of the process. As each animal took part in ten sequential trials, it could be expected that the ability to open the door would improve with each trial. Looking at the results in table 1 there is no sign of improvement over the duration of the trials. This does not take away the fact that the difference in the learning ability between the groups can still be seen as an effect of the incubation temperature because of the limited number of trials each animal was given. To which side the task was performed did not affect the time taken or the amount of successful openings, and was therefore considered trivial in this study. The results this study looked at was whether there was a difference in social learning ability after incubation at different temperatures - not how the animals learned from the demonstrator - and therefore the slight variation in door appearance between the demonstration video and the test-door was considered negligible. In addition, the effect of a difference in the test apparatus was identical for both groups, so the results showing a difference in time taken to open the test-door are still considered to be valid. Both groups were successful in opening the test-door, using stimulus or local enhancement, which shows that both groups of bearded dragons were capable of social learning. However, the time it took to perform the task successfully may have been shorter in both groups if the test-door had been identical to the one used in the demonstration video. This also raises the question whether the cold incubated animals were quicker to make the connection between the test-door shown in the demonstration and the one in the test apparatus, and were therefore faster learners rather than more capable of social learning. If the cold group indeed understood the similarity faster, it would mean that incubation temperature also influences intelligence. To test this hypothesis additional studies would need to be designed.

A potential shortcoming of this study is the lack of a control group for each incubation temperature that had to solve the task without first watching a demonstrator. Due to the lack of animals such a group was not included, but ideally it could have been used to pull apart the results of two groups. Such a control group was deemed not necessary for this study as clear differences have been observed. For more clarity in future studies, inclusion of a specific control group without a demonstrator should be considered to help interpret any findings in the data.

Conclusion

What mechanisms of social learning bearded dragons use will need further research, as well as the reason for the difference in social learning performance between the incubation groups. This study investigated the effect of incubation temperature on social learning abilities and found that the cold incubated animals were faster at learning the task of opening a test-door from a demonstrator than the hot incubated animals, leading to the conclusion that incubation temperature does indeed influence social learning abilities in bearded dragons.

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