The Influence of Body Temperature on Motion Patterns on Anolis Lizard Visual Display

Timothy Fagan

Abstract:

Anolis sagrei has a display in the form of bobbing its head up and down. In order to more accurately understand the communication and honesty of the display two experiments were done. Honesty, in reference to it being an honest signal; meaning that this form of communication is correlated with the condition of the animal. The first experiment examined the lizards in a recreated environment. By controlling the temperature of the setting and recording the interaction we were able to determine how changing the temperature could cause a difference in display. The second experiment examined the lizard's ability to see rapid and sharp movements. By watching lizards' reactions to different frequency dot movements we could determine if changes in speed of a display would be visible to the lizard. In the first experiment, we found that the cold temperature caused the display to be significantly slower than in warmer temperature. In the second experiment, we found that the lizard responded most positively to the faster, more abrupt movements and therefore would be able to notice different speeds of the display. The connection of temperature to the display, as well as the knowledge that it is visible to the lizard, allowed us to conclude that the lizard's display is an honest signal.

Keywords: Motion, Temperature, Signal, Honest display, Lizards, Anolis, Communication

Introduction:

I: Visual Display:

A: The animal kingdom is a vast network and ecosystem full of incoming and outgoing information from a variety of sources. The process of evolution has allowed many different species to relay information, these different types of communication will vary for each species according to their evolutionary track. These communication types are not chosen but created through the generations by making the species better and better at surviving. This allows protection due to the enhanced ability to work together to ward off predators, gather food, and attempt to mate. There are also some species whose form of communication is through competitive interaction of that same species. Some species try to stay as silent as possible, such as when hunting or hiding, while others have come up with specific systems to communicate information. These communicative animals develop this communication mainly in order to give messages to their rivals or potential mates. These messages can be as complex as describing other animals and environments, or as basic as self-identification. Scientists have shown a long-standing interest in understanding the function of signals and the evolutionary forces that lead to their diverse forms. One of the few specific variations of lizard that has evolved to inform information is with the use of a visual display. The lizard is an animal with many different variations, and while most of them have their own form of communication the study will be focusing on one specific lizard that communicates in its own way.

Our study focused on the use of visual displays in the lizard *Anolis sagrei*. This display, similar to all others, has the purpose of communicating information. Although Anolis has a similar display to other lizard species, it is effectively different; this difference is due to differentiating levels of complexity, patterning, and amount of signals (Jensen 1977). Even today we still are not exactly sure of the information that is being communicated, but we know the two scenarios it is mainly used in. The first is when a male encroaches on another male's territory. Instead of fighting immediately, the two individuals use their visual display to attempt to scare off their opponent. If one of the signaling animals can convince the opponent that it is a superior fighter, then the opponent will flee, and the signaler gets the territory without risk of direct fighting. The second context is that males use the display to attract females, and encourage them to mate. Based on these two interactions, it can be assumed that the display is communicating about the health, strength, or genetic quality of the lizard.

B: There are a number of animals that use visual displays in order to convey information, such as fish, mammals, and reptiles. Lizards of the genus *Anolis* use an elaborate temporal pattern known as “Head Bobbing” where their heads will literally move in an up and downward fashion. At the same time as this head movement, the lizard's dewlap (a small colorful piece of skin) will be pushed in and out for further display. Dewlaps come in a variety of different colors such as red, orange, yellow, and blue (Fleishman 1992). The lizards used in our studies (*Anolis sagrei*) have a reddish-orange dewlap. Jennsen (1977) reviewed the diversity and function of *Anolis* motion displays. Jennsen found that a dominant male lizard may raise its head showcasing the colored throat, while a subordinate below will hide its throat showing submission. Clearly, very similar to our *Anolis* lizards showcasing the dewlap. Jennsen concluded from this that the evolutionary origin of these displays could come from a variety of sources. The display could have started as a common response in the somatic nervous system or that regular response in a threatening situation could be a raw material for this now evolved head bobbing. These messages towards a male would therefore be an attempt to show how physically fit they are and can be used to confront an encroaching male in order to stay in the territory Jensen (1977) also found that a display called "jiggling" can be performed in a variety of contexts, including the males signaling to females in mating season. It is clear to say that the visual display and likely the dewlap display would communicate to a female that I am healthy and ready to mate.

C: While we may not fully understand what exactly is being communicated, the head bobbing display is certainly a form of communication. Jenssen (1977) defined displays as body movements that include (1) raising and lowering of the head alongside the extension of the dewlap, (2) are stereotyped, and (3) are generally shared by the population. Since these movements are defined as a type of signaling, it would imply there is a genetic factor. This signaling is not something that is taught or developed while in adolescence. Young anoles begin to display spontaneously, implying that it is inherent within their DNA. According to Jenssen(1977) it is very unlikely that a unique display would evolve *de novo,* meaning it is unlikely to randomly occur from a random gene alteration. Since signaling behavior has evolved in so many species, it is clear that it provides the signaler with some evolutionary advantage. One possibility that would favor its evolution is if the signal movements somehow served as an "honest signal" of fitness.

II: Honest Signaling:

A: Animal communication signals often serve to repel same-sex rivals or attract potential mates. If a signal can help repel a rival, it seems logical that individuals that cannot necessarily defeat a rival might attempt to repel them with threat signals. Similarly, if a signal is attractive to females, any individual is likely to produce it -- whether or not they possess traits that make them attractive. For these reasons, receivers should evolve the capacity to pay attention only to signals that are constrained in some way so that they correlate with some feature of the signal. Signals that can be easily "faked", are likely to be ignored. This should tend to favor the evolution of signals that are either costly to produce (energetic cost, cost of retaliation) or are constrained by physical limitations. Such signals are referred to as "honest signals." Bradbury and Vehrencamp (2011) concluded that this process will lead to a state where most animal signals will, at least to some degree, correlate with important features of the signaller, and therefore be at least partially honest. The hypothesis explains how most signaling in animals is a true form of communication: meaning that if an animal is signaling it is healthy, then it is usually healthy. Some forms of signaling involve aspects or features that cannot be hidden such as the color or vibration of certain bird feathers. The reason it is believed that these signals are not faked more often is that the signals themselves actually require a certain degree of fitness to accomplish. In general, honest signals are expected to be difficult to produce “dishonestly” or involve an elevated fitness cost to a “dishonest” signaler.

In this study we hypothesized that the most rapid and abrupt movements in the head bobbing threat display of *Anolis sagrei* might represent a form of honest signaling. In order to carry out the most rapid movements, a lizard would have to be in a good physical condition. This seems to align with honest signaling since this signal would require physical effort from the lizard, the stronger and healthier the lizard the faster the head bob will appear. The same goes with the color and vibrancy of the dewlap. The dewlap is not something that could be faked, a good coloration would require a balanced meal and good genes. This can only be accomplished by a male who is physically fit enough to get the meal and has good enough genes to warrant a good color. It is also important to take the environment to account.

The display of *Anolis sagrei* consists of a series of very abrupt up and down movements. These animals are behaviorally thermoregulating ectotherms. Assuming that differences in body temperature alter muscle contraction speed and strength, it seems likely that a cooler individual would not be able to move as quickly within the display. Since temperature regulation would also limit their fighting ability, the speed of display movements could possibly represent a physically constrained honest signal of fighting ability -- with regards to body temperature.

III: Influence of Temperature:

A: The signaling of the lizards is highly reliant on the movement and strength of the muscles. It is well known that high and low temperatures can affect an animal's ability to move "Temperature is known to affect whole-organism performance capacities significantly in ectotherms, but may potentially alter performance kinematics as well" (Bennett 1985). With the *Anolis*'s signaling being reliant on their muscles then it is important to find proper temperatures for these muscles. Specifically what allows the lizard to move its muscles to perform the best in the display. Bennett (1985) noted that the *Dipsosaurus* prime body temperature is around 40 degrees. Contractile forces will be accelerated at around 44 degrees in general. The Dipsosaurus is not all together very similar to *Anolis sagrei*, although it does tell that each individual species will likely have its own temperature preferences. Looking at the *Anolis nelsoni*, a closely related species to *Anolis sagrei*, it is more similar in body temp to *Anolis sagrei* than the dipsosaurus. In battling for territories against other males, it would make sense that some of the best territories would have an abundance of food available, female lizards, and a prime temperature. This allows the lizard that hosts the preferred environment a distinct advantage since they would be at ideal temperatures for their signaling. The range of temperatures over which lizard muscles can function is clearly affected by their thermal regimes (Bennett 1985); this simply further exemplifies how important a role temperature has when choosing a territory. It also says that the incumbent lizard will have an advantage over an encroaching lizard. The lizards occupying the area would also have the benefit of being properly fed, energized, and in proper temperature whereas intruding lizards may not have any of this. If an incoming male still somehow had a faster head bobbing signal, it would likely imply they are in better condition regardless of them lacking all the amenities that the incumbent lizard has.

V: Hypothesis and Methods:

In our experiment, we attempted to test three separate hypotheses. The first is that warmer animals, closer to optimal body temperature, should be able to generate faster movement with more abrupt stops and starts. In measuring this aspect we video-recorded the lizard's action during a visual display and analyzed the footage to estimate movement. The second is an animal viewing such patterns should have the capacity to discriminate movements of different speeds;

they should have the sensory capabilities to tell the movements of cold animals from those of warm animals. To test the second hypothesis we had various male lizards in cages and tested them by showing quick movements of a dot created on an analog oscilloscope. This was done in order to see if they are able to see differences in frequency of movement. Finally, that isolated muscle subjected to different temperatures should show changes in its contraction dynamics. We have done this by changing the temperature in the caged animals and recording their display. By analyzing it against its normal body temperature we can see if there's a difference in movement.

Methods and Materials:

The lizards used in the experiments were adult male *Anois sagrei*, captured in the wild in Florida and shipped by a licensed supplier (Snakes at Sunset, Miami Fla.). They were kept in an environmentally controlled room at a temperature of 28ºC, and 52% humidity, and a 14 h light, 10 hours dark-light cycle, each in their own cages. Each lizard was given water once a day and food every other day. The cage included a wooden perch for the lizards to rest on as well as leaves and dirt in order to simulate their normal environment. All the experiments were conducted in approved animal use protocol. In analyzing we found two different things to measure, the rise time and amplitude of the display. Rise time was found by counting the amount of frames each display lasted, with this we created an average rise time for each individual display. The amplitude was found by creating a graph of the display. The top and bottom of the display was measured in the graph to determine the sizes of the display for each individual lizard. From there, the information was compared between warm and cold in order to determine any differences in the temperature displays.

I: Response to Motion Patterns

This part of the experiment took place in the same environmentally controlled room where the lizards were housed. We caged eight lizards separately in a row each at the same height. Each day some of the eight lizards would be given visual stimuli. The visual stimuli given was the vertical motion of a small green dot produced on an analog oscilloscope. The dot movement timing was the same each time. We started with a square wave motion pattern. We used an electronic low pass filter to alter the timing of the dot movement by removing high-frequency components. Movements ranged from abrupt, nearly square waves, to a smoother, slower pattern. The lizards were never tested consecutively; they always had a day of rest. Deciding which lizard to test was based on whether they were in a position to see the visual stimuli from their resting point in the cage. The stimuli were given in the lizard's periphery. Motion Is the strongest stimulus is motion in the peripheral as the lizard only eats moving prey (Fleishman 1986).The oscilloscope was set up at 45^{o} angle to ensure that it was in the lizard's peripheral vision. Once the stimulus device was positioned a few inches away from the cage, we allowed the lizard five minutes to grow accustomed to the device while we were watching from a camera outside the room. Once the time was done we gave three separate trials and marked down if the lizard responded, allowing two minutes between each trial in order for the lizards not to get used to the motion. A response consisted of the lizard looking in the direction of the stimulus within a short time of a couple of seconds. The data was recorded as a negative if there was no movement or a positive if there was a response. Each of these checks were marked and logged throughout the weeks. In order to properly give the stimulus, we would set up the machine and a small camera directly in front of the cage to view the animal's response. There were six total low pass filter frequencies tested, 1, 5, 20, 50, 100 Hz, and a control of no stimulus motion. In order to avoid bias, stimuli were delivered in random order. Each stimulus was delivered once before any were repeated. This was done daily throughout the year to get our full data set.

II: Generating a display

The second part of the experiment had two different lizards brought to a different temperature controlled environment. Each was again put into a cage, and they were given a few days to grow accustomed to the environment. Similar to the other room they were watered once a day and fed crickets every other day. Once accustomed to the warm or cool environment we would bring in another male taped to a stick. Each session for each lizard lasted 20 minutes and was recorded with a 60 FPS camera. Specifically, the moments of clear signaling were recorded and analyzed with motion processing software. With this software, we could measure the movement of the displaying lizards. After weeks of testing both hot and cold a data set could be made from this information and analyzed statistically. At least 10 lizards will be tested at both cold and warm temperatures and have their movements measured. Once all the recordings were done they needed to be properly analyzed. We would cut out the few seconds of display within each 20 minute video. Using this and a program called MatLab we were able to graph the up and downs of the display.

Results:

I: Animal Viewing pattern

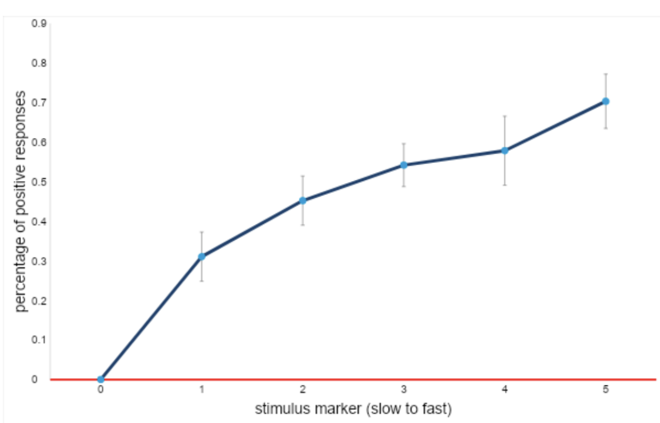

Figure one shows a rate of positive responses to the moving stimulus as is presented to them. The control of zero got no positive responses, while frequencies one through five got increasingly higher with increasingly more positive responses. From one to five the Hz increased by: 1, 5, 20, 50 100. The fastest frequency getting the most positive responses implies that the lizard would be able to see the differences in speed of display.

II: Generating a display:

In generating a display two different measurements were taken, the height of the display and the time of the display. Height refers to the distance from the bottom of a head movement to the top of a head movement. As seen in Figure 2 the cold and warm temperature lizards' differences in heights are not significant. While the bar for cold is higher, the p-value being .65 shows that they do not have any significance.

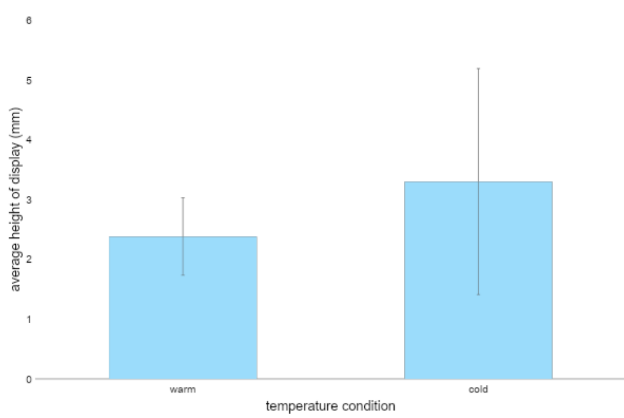

Figure 2. The average height of visual display movements at warm and cold temperature conditions. A t-test revealed that there was no significant difference in height of displays in warm and cold lizards, p=0.65

Figure three shows the difference in timing between the warm and cold displays. Rise time refers to the amount of time it took for the head bob to go from the lowest point to the highest point. The differences are not as pronounced as seen in figure 2, but they are significant. This significance shows that the colder lizards are in worse

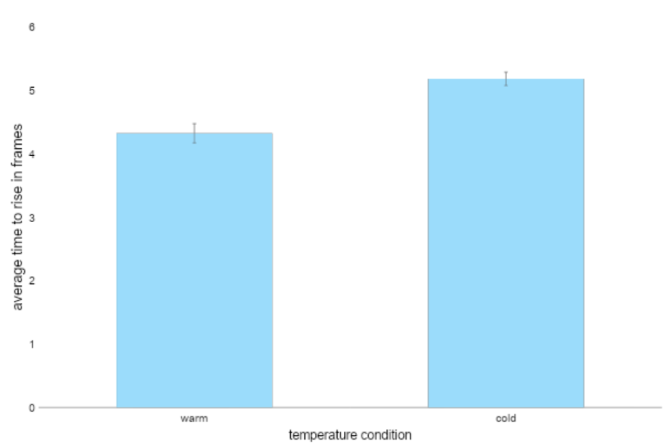

Figure 3. The average rise time in frame rate for lizards to reach the top of their display in warm and cold temperature conditions. A t-test revealed that there was a significant difference in rise time in warm vs. cold lizards, p=0.0006

conditions than warmer ones and will therefore display slower.

Discussion:

I: Further detail

Looking at figure one, it is shown that the lizards can see differences in the speed of displays. This ability makes sense, the anoles have large eyes relative to their body with a wide peripheral view (Fleishman 1986) implying that they are highly dependent on seeing fast movement. This dependence on fast movement is shown by comparing the amount of positive responses in the different frequencies. The fastest frequency got the most positive responses while the slower ones got less positive responses. This would imply that the lizard can notice fast differences easier than slower differences. This is understandable, as motion is important to the anolis, they generally eat moving prey, they detect predators through movement, and communicate through the head bobbing motion (Fleishman 1986). Had the lizard gotten more positives in the slower frequencies, that would mean they could not see differences and therefore these differences in the display are not a factor in anything. Regardless of the reason for the lizard having this ability, it allows the lizard to see differences in the display. Meaning, that a male would be able to interpret another male's display as them being very strong or very weak. From that point of the interpretation, the lizard would decide on the course of action either to attack or run away.

The second graph does not give significant information yet still opens up some interesting ideas to the experiment. We already know that the lizard being ectotherms causes their reliance on outside sources for warmth. The sprint speed and other locomotor capacities will correspond with body temperature, this would mean that any performance would be limited due to the thermal environment (Lailvaux, Irschick. 2007). Now while the difference in height of the display was not significant, it is possible this could have been due to a limited number of test subjects. Possible further research with a greater number of lizards may find that the cold do significantly have a larger height in display. The reason I put this possibility out is because it would help clarify how cold actually affects the lizard's body. If the cold simply tenses the muscles and that is why it slows, then the non significance makes sense. Whereas, if the cold somehow affects the actual neurotransmitters that signal for motion, then it is possible the delay in signaling would cause a significantly larger display. This is all simply ideas for further research but the ideas are important to keep in mind for further explanation on colds affecting the anolis.

The third graph confirms the necessity of the ability to see differences in speed by showing that the warm and cold displays are significantly different. In order to understand the function of the signal and evolutionary process used to make them, understanding the information conveyed in these visual displays is vital (Qui, et al 2021). A lizard whose body temperature is not at its preferred value will tend to be weaker and slower than in warm conditions. Understanding the range of temperatures that a species experiences as well as preferred body temperature is needed to properly test temperature effects on performance (Lailvaux, Irschick. 2007). In order to see the lizards' realistic reactions, seeing them in both warm and cold allows for a proper examination of the signaling. It is also assumed that the lizards receiving the signal would be assessing the quality from whatever information is contained and will respond appropriately (Qui, et al 2021). The original hypothesis of honest signaling is dependent on the animal's condition being linked to the animal's ability to communicate. With this part of the experiment, we showed how the *Anolis*'s head bobbing display is tied with the animal's condition. This is shown through the differences in speed in different temperatures. Since the communication and condition are tied, we can say that the animal's display pattern is an honest signal.

It is important to remember that the hypothesized reason for these displays is so the lizards can avoid fighting when possible. If a lizard can see that a male is significantly stronger or faster than they are based on the speed of their display then the option to run away will be more effective. Whereas, if a lizard is unable to see differences in the display, then the only basis of condition would be for the lizards to fight and see who survives. Of course, regardless of seeing the display, the fighting does still usually happen; this is likely due to any differences in display not being large enough to scare off any male. Even with the fighting still occurring, it is a good way to avoid pointless fights. Even if a male in great condition attacks a male in the horrible condition it would still leave them both vulnerable for some time. This would put the male in better condition in an unnecessary risk for other males coming in, predators getting the drop on them, or accidentally sustaining injury. Therefore, while it is not used to avoid fighting every time it allows for unnecessary risk to be mitigated through these observations of display

II: Problems in research & ideas for future research

Like any research, there have been a few bumps in the road and some areas that future researchers can possibly improve upon. The main problem as is in any research is the amount of data collected. While we were able to test a good amount of lizards in each experiment, many of the lizards in the temperature experiment were not very cooperative. This somewhat limited the amount of data that we could actually use. It is important to note that when recording we would use a large sheet that hid our bodies, we did this in order to not scare the lizards with our bodies constantly moving around them. Keep in mind, to understand how temperature affects ectotherms such as the anolis you need to adapt both laboratory and in field approaches (S.P. Lailvaux, D.J. Irschick. 2007). Therefore, putting them in a comfortable environment without constant supervision will likely lead to better results. We allowed the lizards at least a week in order to get used to the environment prior to the addition of the invading male. Without this adjustment time, we found that getting any data was quite difficult. For the visual display pattern experiment, the problem was similar. While we used the same lizards over the course of the year there were a few that simply would not get into proper position or would hide. To avoid this from happening it could be helpful to take away any covering the lizard could use to hide and to allow for the lizard to be viewed in any position inside the cage.

In the future, researchers reattempting this experiment may want to change some things to look for different or more specific answers. In the temperature experiment, the way the incoming male is allowed in can be changed. We started out with having the male tied down, but towards the end we simply let the male be free in the new environment. Focusing on one method, or creating a new one could possibly allow for better results. Another idea that could change the data is using temperature differences in the visual display experiment. Simply do the experiment again, but have some of the lizards in colder temperatures while doing so. This could help understand how cold may also affect the lizard's vision instead of simply their internal muscles

III: Conclusion

The three hypotheses were given a good amount of data to help support the ideas. With the first being that warmer animals would move faster, the second that the animals would be able to discriminate between fast movements, and the third that isolated muscles would change contraction dynamics in different temperatures. The first and third hypothesis was supported by the testing and recording of displays at different body temperatures. The testing allowed us to see how the display would be affected in various temperatures. Through this experiment, we saw exactly what we were hypothesizing, that the display speeds up in the warm and slows down in the cold. The second hypothesis was supported through the tracking of the lizards viewing fast and slow frequencies. Again, we observed what we originally expected, that the faster and more abrupt movement was noticed more than the slower movement was. While none of this can be used to confirm anything it can be used for the help of future research to further determine the nature of Anolis lizard's visual display.

References:

Bennett, A. (1985). Temperature and Muscle. *Journal of Experimental Biology*, 115: 333-344.

Bradbury, J. and Vehrencamp, S. (2011). Principles of Animal Communication. Sunderland, MA: Sinauer Associates, Inc.

Fleishman, L. (1992). The Influence of the Sensory System and the Environment on Motion Patterns in the Visual Displays of Anoline Lizards and Other Vertebrates. The American Naturalist, 139: 36-61.

Fleishman, L. (1986). Motion detection in the presence and absence of background motion in an *Anolis* lizard. *Journal of Comparative Physiology*, 159: 711-720.

Jenssen, T. (1977). Evolution of Anoline Lizard Display Behavior. *American Zoologist,* 17(1): 203-215.

Lailvaux, S. and Irschick, D. (2007). Effects of Temperature and Sex on Jump Performance and Biomechanics in the Lizard *Anolis carolinensis*. *Functional Ecology,* 21(3): 534-543.

Qiu, X., Hu, Q., Peters, R., Yue, B., Fu, J., and Qi, Y. (2021). Unraveling the content of tail displays in an Asian agamid lizard. *Behavioral Ecology and Sociobiology*, 75(117).