Spring 5-2021

Is the Dewlap an Honest Signal of Fighting Ability in the Male Green Anole (Anolis Carolinensis)?

Alexia Hughes
Winthrop University, livetogive9799@aol.com

Recommended Citation
Hughes, Alexia, "Is the Dewlap an Honest Signal of Fighting Ability in the Male Green Anole (Anolis Carolinensis)?" (2021). *Graduate Theses*. 131.
https://digitalcommons.winthrop.edu/graduatetheses/131

May 2021

To the Dean of the Graduate School:

We are submitting a thesis written by Alexia Hughes entitled *Is the Dewlap an Honest Signal of Fighting Ability in the Male Green Anole (Anolis carolinensis)?*

We recommend acceptance in partial fulfillment of the requirements for the degree of a Master of Science in Biology.

Dr. William Rogers, Thesis Advisor

Dr. Janice Chism, Committee Member

Dr. Kristi Westover, Committee Member

Dr. Salvatore Blair, Committee Member

Dr. Takita Sumter, Dean, College of Arts and Sciences

Jack E. DeRochi, Dean, Graduate School

IS THE DEWLAP AN HONEST SIGNAL OF FIGHTING ABILITY IN THE MALE GREEN ANOLE (*ANOLIS CAROLINENSIS)?*

A Thesis

Presented to the Faculty

Of the

College of Arts and Sciences

In Partial Fulfillment

Of the

Requirements for the Degree

Of

Master of Science

In Biology

Winthrop University

May, 2021

By

Alexia Hughes

Abstract

Signals are morphological or behavioral traits that an individual uses to influence the behavior or actions of another. These signals can be used in male-male competition, in which male secondary sexual traits act as a signal of his fighting ability. Animal signals are considered honest when the signal reliably indicates a specific trait or condition of the individual. The genus *Anolis,* comprised of over 400 species that occupy the tropics and the southeastern United States, utilize aggressive signaling prior to physical combat. Research on several tropical species of anole indicates that the size of their dewlap can act as an honest signal of their fighting ability, as dewlap size is correlated with the chance of an individual winning in combat. No studies of this nature, however, have been done for the green anole, *Anolis carolinensis.* In this study, I measured the size of adult male green anole's dewlaps, their bite forces, and performed dyadic interactions between two males matched for body size to determine if the dewlap can be considered an honest signal of fighting ability. I found that dewlap size, mean bite force, and maximum bite force did not differ between winners and losers of dyadic interactions. However, latency to bite did differ between winners and losers, and there was a predictive relationship between dewlap size and latency to bite. These results could be explained by the different personalities of male green anoles, specifically regarding an individual's level of boldness. Being bold in a high-risk situation, such as in male-male competition, is dangerous for an individual and comes with the chance of injury or death. The dewlap of the male green anole could potentially act as an honest signal of his cautiousness, and his hesitancy to engage in male-male competition, but also his confidence in his capacity to defeat his opponent if the conflict reaches the actual combat stage.

Acknowledgements

First and foremost, I would like to thank Dr. Rogers for his patience, understanding, support, and endless guidance throughout the duration of my research. Without his help, no part of this project would have been possible.

I would like to thank Dr. Chism, Dr. Westover, and Dr. Blair for their help through the editing and perfection of my writing.

I would like to thank my parents and my brother for their constant love, support, and patience as they listened to me stress and complain.

Finally, I would like to thank Jiggy, who kept me company during my long hours of writing and stressing. Her cuddles helped me tremendously.

Table of Contents

Abstract *Page i*

Acknowledgements *Page iii*

Introduction *Page 1*

Materials and Methods *Page 11*

Study Animals and Their Housing *Page 11*

Measurement of Dewlap Size *Page 12*

Measurement of Bite Force *Page 13*

Dyadic Interactions *Page 14*

Statistical Analyses *Page 19*

Results *Page 20*

Discussion *Page 28*

Literature Cited *Page 39*

List of Tables

Table 1. Matched pairs for dyadic interactions. *Page 16*

Table 2. List of main findings. *Page 29*

List of Illustrations

Figure 1. Example bite force recording. *Page 14*

Figure 2. Interaction tank. *Page 15*

Figure 3. Depictions of aggressive displays/actions. *Page 18*

Figure 4. Mean dewlap weight of winners and losers of dyadic interactions. *Page 20*

Figure 5. Mean bite force of winners and losers of dyadic interactions. *Page 21*

Figure 6. Maximum bite force of winners and losers of dyadic interactions. *Page 22*

Figure 7. Linear regression of a male’s snout-vent length and dewlap size. *Page 23*

Figure 8. Linear regression of a male’s dewlap size and mean bite force. *Page 24*

Figure 9. Linear regression of a male’s dewlap size and maximum bite force. *Page 25*

Figure 10. Mean latency to bite of winners and losers of dyadic interactions. *Page 26*

Figure 11. Linear regression of a male’s dewlap size and latency to bite. *Page 27*

Introduction

Signals are morphological or behavioral traits specialized for communication that an organism (the signaler) uses to influence the behavior of another individual (the receiver) (Henningsen and Irschick 2012; Krebs and Davies 1997). Signals can be used to communicate information about the surrounding environment, such as songbirds (suborder Passeri) who signal to others that predators are near or bees (*Anthophila spp.)* “dancing” to communicate the position of food to their hive mates (Dawkins and Krebs 2004). Signals can also be used to advertise a specific trait or condition of the signaler, such as aggressive level, age, or hierarchical status (Henningsen and Irschick 2012). For instance, dogs *(Canis lupus familiaris)* bare their teeth to indicate their aggressive intent, golden poison frogs (*Phyllobates terribilis)* are brightly colored to warn predators of their toxicity, and many species utilize pheromones to communicate their readiness to mate (Dawkins and Krebs 2004).

In many species, signals are used in intraspecific male-male conflict; male weapons and enlarged or ornamented secondary sexual traits act as threat displays to signal strength and the likelihood of an individual’s winning during physical combat (Vanhooydonck et al. 2005a; Wilson et al. 2007). Rather than immediately resorting to physical force, individuals can use signals from their competitors to gauge their relative strength, retreating if the competitor is perceived as too powerful (Lailvaux et al. 2012; Wilson et al. 2007). Utilizing signaling prior to aggressive encounters reduces unnecessary energy expenditure and the chance of injury or death of the individuals involved. For example, male mandrills (*Mandrillus sphinx)* employ facial signals and gestures to display their dominance to an opponent. In a study of the aggressive interactions among two semi-free-ranging colonies, only 10% of male mandrills who engaged in signaling resorted to physical combat (Setchell and Wickings 2005). Additionally, the song sparrow (*Melospiza melodia)* incorporates signaling during territorial disputes to display aggressive intent. Rather than resort to physical combat, the song sparrows involved in a dispute communicate through a graded series of matched displays; the loser of the interaction is the individual who is unable to replicate the signal given by the opponent, thereby ending the conflict without resorting to physical combat (Searcy et al. 2014).

The evolution of male weapons and enhanced secondary sexual traits is primarily driven by sexual selection (Emlen 2008). When choosing a mate, females of many species prefer males that have an extravagantly ornamented secondary sexual trait (Kirkpatrick 1987). For instance, female barn swallows *(Hirundo rustica)* prefer to mate with males with symmetrical tail streamers; in a field study of a barn swallow population in Israel, tail streamer symmetry was positively correlated with male reproductive success (Vortaman et al. 2011). Hypotheses for why females prefer to mate with highly ornamented males vary, including highly ornamented males being able to provide material advantages, the ornaments reflecting the male's genetic quality, or the ornaments being a by-product of natural selection (Andersson and Simmons 2006). Despite several hypotheses for the evolution of male ornamentation, the overarching consensus is that a highly ornamented male possesses strong genes or has strong reproductive ability (Sullivan-Beckers and Cocroft 2010). Female mate choice, in turn, leads to the evolution of male weaponry, as males compete for access to females. In order for males to gain access to as many females as possible, they may engage in male-male competition to displace rivals (Emlen 2008). Males may compete for territories occupied by females, control over resources needed by the female, or simply prevent other males from gaining access to females (Emlen 2008). Male secondary sexual traits and weaponry may have evolved through the interaction of female choice and male-male competition in response to this female choice, leading to their use as signals of their reproductive fitness and ability to fight off other males for access to females (Sullivan-Beckers and Cocroft 2010).

A signal is considered "honest" when it is consistently correlated with a specific trait of the signaler (Henningsen and Irschick 2012). In the context of male-male competition, an honest signal is one which reliably functions as an indicator of a male's dominance or fighting ability (Vanhooydonck et al. 2005a). In the male three-spined stickleback (*Gasterosteus aculeatus)*, red coloration directly relates to an individual's dominance and territoriality; during male-male competition, brightly colored males are perceived as more dominant and territorial, and lesser colored males retreat to conserve energy and avoid potential injury (Candolin 2000). Furthermore, the intensity and frequency of an honest signal may change to reflect physiological or behavioral changes in an organism (Pentland 2010). For instance, the call frequency of a male cricket frog (*Acris crepitans)* is an honest signal of his overall fighting abilities, and changes as his likelihood of winning a fight changes (Wagner 1992). If a male receives a high-density call (a call coming from multiple cricket frogs) or a call that he perceives as close by, he will increase the frequency of his call to signal more aggressive intent. If the male receives a low-density call or a call he perceives to be from a competitor far away, he will reduce the frequency of his own call (Wagner 1992).

Members of the genus *Anolis*, a diverse group of iguanine lizards, have been widely studied in terms of their behavioral signals. Around 50 million years ago, *Anolis* lizards radiated from Cuba, Jamaica, Puerto Rico, and Hispaniola; today, *Anolis* species are found in the Caribbean, Central America, northern South America, and one species in the southeastern United States (Jenssen 1977). Most *Anolis* species are grey, brown, or green, and span between 35-190 mm in length and 1-140 grams in mass (Losos and Schneider 2009). They are insectivorous, and have enlarged digit and toe pads that allow them to inhabit canopies and vegetation. Their predators include large spiders, snakes, frogs, birds, and some mammalian species (Johnson and Wade 2011). *Anolis* species are highly polygynous, and males rely on competition to increase their control of territories and access to mates (Tokarz 1998). *Anolis* lizards have invaded a wide range of ecological niches, with the attendant morphological and physiological variations we would expect (Williams and Rand 1977; Lovern et al. 2004). However, despite this diversity, they have retained a relatively small number of aggressive displays (Driessens et al. 2014). Studies on the *Anolis* display behaviors include field and lab studies involving the brown anole (*Anolis sagrei)* (Driessens et al. 2014; Jenssen 1977), lab studies on the Jamaican anole (*Anolis grahami)* (Greengerg 1977; Vanhooydonck et al. 2005a), and field and lab studies on the green anole (*Anolis carolinensis)* (Vanhooydonck et al. 2005b; Henningsen and Irschick 2012).

The repertoire of *Anolis* aggressive signaling involves four main displays: lateral displays, head-bobs, push-ups, and dewlap extensions (Driessens et al. 2014). Prior to utilizing other signals, individuals tend to position themselves laterally, a position thought to maximize the visual cues perceived by the opponent (Jenssen 1977). Head-bobs are defined as rapidly moving the head up and down. This rapid, vertical movement is easier for opponents to see over long distances rather than the size or color of the lizard, making this display a prominent feature for the visually-orientated *Anolis* lizards (Fleishman 1992). Push-ups involve the rapid flexion of either two or all four legs during an aggressive encounter (Greenberg 1977). The dewlap and dewlap extensions, the primary focus of my research, are explained in further detail below. Although there may be species-specific variation and modification of these signal types, these four displays serve as the baseline for most *Anolis* aggressive encounters (Fleishman 1992).

The dewlap is an extension of the gular flap, a granular fold found on the ventral throat in front of the forelegs. It is an extensively studied feature of the *Anolis* genus. It is a sexually dimorphic trait that in most *Anolis* species is only present on the male (Deperno and Cooper 1994), although in some species it is either present on the female or non-existent in either sex.

In addition to male-male encounters, anoles utilize the dewlap during male-female interactions, predator encounters, and non-directed displays (displays performed when no conspecific neighbors are present or detected by the signaler) (Henningsen and Irschick 2012, Vanhooydonck et al. 2005b). *Anolis* male-male interactions involve a combination of the displays described above, along with frequent utilization of dewlap extensions.

During male-male interactions, *Anolis* lizards extend the dewlap, increasing the apparent size of the signaler; these dewlap extensions are considered a “challenge” or “threat” to their opponents (Vanhooydonck et al. 2005a, Jenssen 1977). Its use as a display during male-male competitions makes the dewlap a convenient structure for research for honest signaling. While studies have been done concerning the honesty of the dewlap as a signal of fighting abilities in the brown anole (*Anolis sagrei)* and several Jamaican anoles (*Anolis lineatopus, Anolis grahami, Anolis valencienni)*, no studies of that nature have been performed on the green anole, *Anolis carolinensis.*

Anolis carolinensis is common in the southeastern United States and is a sexually dimorphic, highly territorial lizard whose behavioral patterns have been extensively studied (Henningsen and Irschick 2012). Males are around 1.5 times larger than the females, and have dewlaps that are used in aggressive displays during male-male competition (Bloch and Irschick 2005, Vanhooydonck et al. 2005a, Vanhooydonck et al. 2005b). Female green anoles do not have a dewlap (Greenberg and Noble 1944). Both sexes can alter their body color from green to brown, depending on environmental conditions as well as inter-individual interactions (Conant and Collins 1991). Although this coloration is primarily used for camouflage, in an aggressive encounter a green individual is generally dominant, while a brown individual is submissive (Conant and Collins 1991).

Some research suggests that sexually mature green anole males can be divided into two morphological classes: a smaller, weaker male, referred to as a “lightweight”, and a larger, stronger male, referred to as a “heavyweight” (Lailvaux et al. 2004). Bite force is related to the size of the lizard: larger males have proportionally larger jaws, giving them a stronger bite force than smaller males with smaller jaws (Lailvaux et al. 2004). That work found that the two classes fall along the same growth curve, suggesting they are actually life-history stages of the sexually maturing male. A younger male, with his smaller body size, has smaller jaws and a weaker bite force. As the male matures, he increases in body and head size, creating a proportional increase in bite force. Although both classes display slightly different fighting strategies during physical aggressive encounters, they both utilize dewlap extensions during signaling (Vanhooydonck et al. 2005a)

Jenssen et al. (1995) found that free-ranging males, during the breeding season, primarily utilize a territory to attract females, focusing their attention on breeding displays and protecting the territory from invading males. During the non-breeding months, more energy was directed towards foraging behavior and predator avoidance, with little emphasis on protecting their territory from invading males. During April and May, the breeding months, green anole males engage in combat at the edges of their territories to defend those spaces or to obtain a portion of a neighboring male's territory to increase their access to females (Medvin 1990). During aggressive encounters that result in a physical fight, male *A. carolinensis* tend to rely on two primary strategies. Smaller males, with a relatively weaker bite force, are likely to rely on their locomotor abilities to maintain control over their territory. Locomotor quickness enables a lightweight male to obtain a perch quicker than a slower opponent and subsequently maintain it for longer. Larger males with their stronger bite force rely on physically fighting their competitors (Lailvaux et al. 2004). The most aggressive form of a physical encounter between two males involves jaw-sparring, where one of the males clamps onto and holds the other until the bitten animal submits (Greenberg 1977). This would predict that, if a physical encounter is to occur between two males, the male with the stronger bite force should win, as he is more capable of holding onto an opponent until the opponent signals submission.

Many lines of evidence suggest there is a link between an individual's relative bite force and its fighting abilities. Observations of male *A. carolinensis* during aggressive encounters have shown they primarily rely on biting, jaw-sparring, and sometimes slamming their opponent against the ground or other substrate (Vanhooydonck et al. 2005b). One could expect that males with a stronger bite force would have an advantage over those with a weaker bite, and therefore increased overall fighting ability, an assumption supported by Lailvaux et al. (2004) who found that males with a stronger bite force were more likely to win dyadic interactions versus those with a weaker bite force. Additionally, there is a link between head size and ability to win male-male encounters; because head size is proportional to bite force, and thus one can expect bite force to be responsible for this link (Herrel et al. 1999). Furthermore, Lailvaux et al. (2014) found a correlation between dewlap size and bite force; larger males have larger dewlaps and tend to have a stronger bite force.

Despite these findings, there are very few studies that examine whether dewlap size is an honest indicator of fighting abilities in *Anolis carolinensis.* Although experimental research has shown this to be the case in other *Anolis* species (such as in three Jamaican *Anolis* species, see Vanhooydonck et al. 2005a) no studies of this nature exist for the green anole. Additionally, the green anole is an interesting species because of its geographic range. Similar to other *Anolis* species, green anoles are ectotherms who are active in the warmer months, when the sun provides the heat necessary for homeostasis. Other *Anolis* species, which live in the tropics, can generally be active year-round. The green anole, however, is the only *Anolis* species that lives in the Southeastern United States, where they experience colder winters and harsher conditions than species that live in the tropics. This creates an intriguing scenario: the green anole has a more constrained reproductive window than other *Anolis* species, increasing the importance of a male procuring as many females as possible to increase his reproductive success. In this study, I propose to measure the bite force of male *Anolis carolinensis* to determine whether dewlap size is an honest signal of bite force. Furthermore, I will measure fighting abilities by setting up dyadic encounters between males of varying dewlap size to determine whether dewlap size is an honest signal of fighting abilities.

Based on previous research that shows there is a correlation between dewlap size, bite force, and fighting abilities in other *Anolis* species (Lailvaux et al. 2014; Lailvaux et al. 2004; Herrel et al. 1999; Vanhooydonck et al. 2005a), as well as the use of the dewlap in the repertoire of signals during aggressive encounters (Vanhooydonck et al. 2005a), I tested two hypotheses. I predicted that males with larger dewlaps will have a stronger bite force than males with smaller dewlaps, indicating that dewlap size is an honest signal of bite force. Additionally, I predicted that males with a larger dewlap will win more dyadic interactions than males with a smaller dewlap, indicating that dewlap size is an honest signal of fighting ability.

Materials and Methods

Study Animals and Their Housing

All procedures were approved by Winthrop University's Institutional Animal Care Committee protocol #IACUC20002. A total of 36 adult male *A. carolinensis* were ordered in three groups of 12 from Carolina Biological Supply (item number 147240) between August and October of 2020. The lizards were confirmed to be male by the presence of postanal scales, two large scales at the base of the tail that are only present in males. Six adult, female *A. carolinensis* were ordered from Carolina Biological Supply (item number 147244) in September 2020. All lizards were housed in Dalton Hall at Winthrop University, Rock Hill, S.C. 29733. Upon arrival, the animals were weighed and their snout-vent lengths (SVL) were measured. Weight (g) was taken by placing individual lizards in a sealable plastic bag, removing the air for approximately 30 seconds, and placing the bag on a tared scale. SVL was taken by measuring the distance from the tip of the snout to the cloaca. After measurements were recorded to the nearest mm, each lizard was tagged with a black felt tip marker by writing a number on its stomach and using a unique pattern on its toes for identification. For example, male 1 was marked with a "1" on his stomach and had both front outermost toes colored. This was an appropriate nonpermanent identification technique as the marks are lost when the lizard sheds its skin.

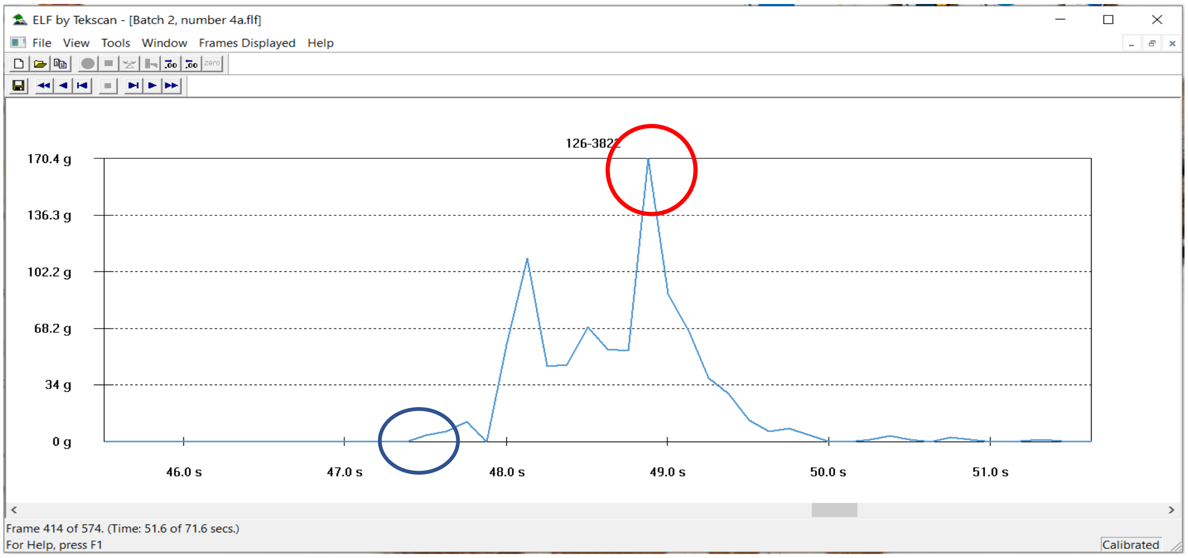
Male lizards were housed in individual 37.85L tanks. Prior to experimentation, each tank was cleaned with a 1mL:1000mL acetic acid to water solution to remove calcium build-up in the tanks. After the tanks air dried, each was filled with approximately 1.3 centimeters of gravel to cover the bottom of the tank, 3-4 sticks collected from the woods near Winthrop University to make a perch, one large rock for a basking area, and two plastic trees. Each tank was illuminated by a UV lamp (Zoo Med Repti Basking Reptile Spot Lamp, Item #99049) with a 75-watt basking bulb on a 14:10 light-dark cycle. Male tanks had cardboard panels on both sides to keep the animals visually isolated from one another. All six females were housed in a single 37.85L tank set up in an identical fashion to the males' tanks, and were also visually isolated from the males on either side of their tank. Lizards were fed with waxworms (*Galleria mellonella)* to satiation and misted with water once a day. After experimentation was complete, lizards were released into Winthrop Woods, as the southeastern United States is well within their natural range.

Measurement of Dewlap Size

Dewlaps of all males were measured upon the animals' arrival. Each lizard was positioned with its gular area abutting and parallel to an edge of a sheet of graph paper. The dewlap was gently, but maximally, extended by hand, and an outline was traced with a pencil onto the graph paper. After all dewlaps had been traced, the graph paper was photocopied in order to have a backup copy in case the original was lost. Each original dewlap trace was labeled, cut out, and then weighed (g), with the weight acting as a proxy for dewlap area.

Measurement of Bite Force

Bite force of the male lizards was measured using the FlexIForce ® ELF Load and Force Measurement system (Kistler, Wintherthur, Switzerland) upon their arrival to Winthrop. Prior to bite force measurement, the Load and Force system was calibrated using the protocols included with the FlexIForce system. Each lizard was prompted to bite the free end of the probe by gently prying its mouth open by hand. Once the mouth was open, I removed my hand and the probe was placed in the animal's mouth to avoid human interference in the measurement. The lizard was allowed to bite the probe until he naturally removed their mouth from it. The bite force of each lizard was taken one time, and each male bit the probe multiple times during the trial. The number of bites per trial ranged from 1-10. All bite force measurements were recorded (in g) using the ELF Multi-handle software (v 4.33), the Windows program used to record measurements from the Load and Measurement system. Maximum bite force for each individual was considered the strongest bite during its recording. Absolute latency was calculated as the amount of time it took each individual to initiate biting the probe. Relative latency was calculated as the amount of time between the individual's first bite and its strongest bite. For reference, as shown in Figure 1 below, the blue circle indicates the absolute latency for this individual, which occurred at approximately 47.5 seconds. The red circle indicates the maximum bite force for this individual, which occurred at approximately 49 seconds. Thus, the relative latency of this individual is 1.5 seconds.



Frame 414 of 574. (Time: 51.6 of 71.6 secs.)
For Help, press F1

Figure 1. Example showing the maximum bite force (red circle), absolute latency (blue circle), and relative latency (calculated as the time from absolute latency to maximum bite force).

Dyadic Interactions

To test the hypothesis that males with larger dewlaps would win more combats, I staged a series of dyadic interactions. Dyadic interactions took place in a neutral 37.85L tank separate from the individual housing tanks. The combat tank had a removable, opaque, plastic barrier that bisected it at the midpoint of the long sides, creating two equal halves. Each half of the tank was a mirror image of the other and was furnished in the same fashion as the housing tanks (Figure 2). Each half of the tank also had a female lizard (matched for weight, SVL, and health) to further increase each male's level of territoriality. The same two females were used for all dyadic interactions. Rival males were always within three mm of each other's snout vent length, and in 10 of the 15 interactions performed, rival males had identical SVL (Table 1). In preparation for an interaction, one male was placed on either side of the tank, with a female and with the opaque divider present. The animals were given a three-day acclimation period upon introduction to the interaction tank. After the acclimation period, the opaque divider was removed, allowing the males and females to interact with one another.

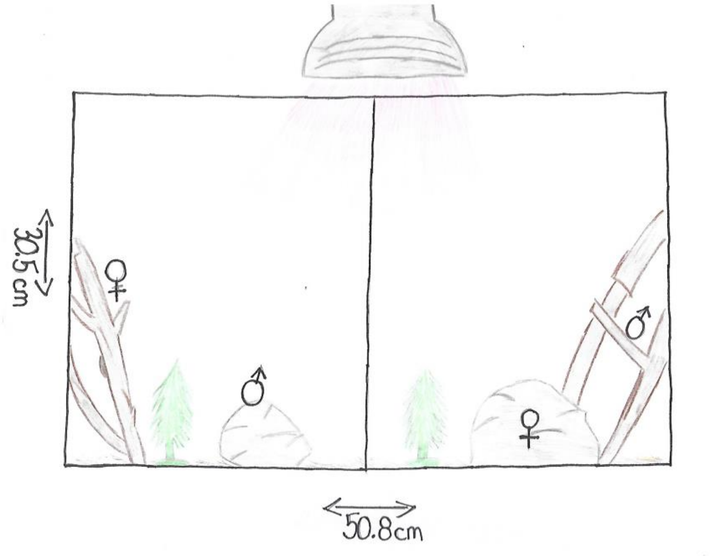


Figure 2. Diagram of the interaction tank.

Batch	**Matched Pair**	**Snout-Vent Length (mm)**	**Dewlap (g)**
I	1, 11	56, 56	0.005, 0.006
I	2, 4	58, 58	0.010, 0.005
I	9, 12	61, 61	0.009, 0.009
I	5, 13	62, 62	0.018, 0.007
I	7, 8	64, 64	0.012, 0.005
II	7, 11	65, 66	0.013, 0.004
II	5, 10	63, 64	0.007, 0.009
II	1, 4	60, 62	0.006, 0.007
II	3, 9	59, 57	0.004, 0.007
II	8, 12	53, 51	0.005, 0.006
III	1, 4	48, 48	0.005, 0.002
III	3, 12	52, 52	0.005, 0.003
III	8, 9	53, 53	0.005, 0.005
III	2, 11	55, 55	0.007, 0.003
III	5, 7	61, 61	0.004, 0.007

Table 1. Matched pairs for dyadic interactions. Rival males had snout-vent lengths within 3 mm of each other. Batch number refers to which of the three groups the lizards were involved in. Matched pair refers to which lizards from each batch were paired for the dyadic interaction.

The lizards were allowed to interact for one hour, during which they were monitored and the males' aggressive actions recorded. Aggressive actions were scored based on standard protocols detailed in Perry et al. (2002), Lailvaux et al. (2004), and Henningsen and Irschick (2012) to allow for comparisons with other studies. Push-ups, dewlap extensions, and head-bobs were assigned a score of 0.5. Lateral displays, chasing, and biting were assigned a score of 1 (Figure 3 provides an illustration of the displays). At the end of the hour, the total score for each male was calculated. The winner for each interaction was considered the male that had the higher overall score. The interactions where males had a tied score were excluded from the statistical analyses. After the interactions, the males were placed back in their respective individual tanks and the opaque divider was replaced. Females were placed back on their respective sides. After the dyadic interactions for each batch were complete, the males were released into the wild prior to the next batch arriving to Winthrop, so each lizard only participated in one dyadic interaction.

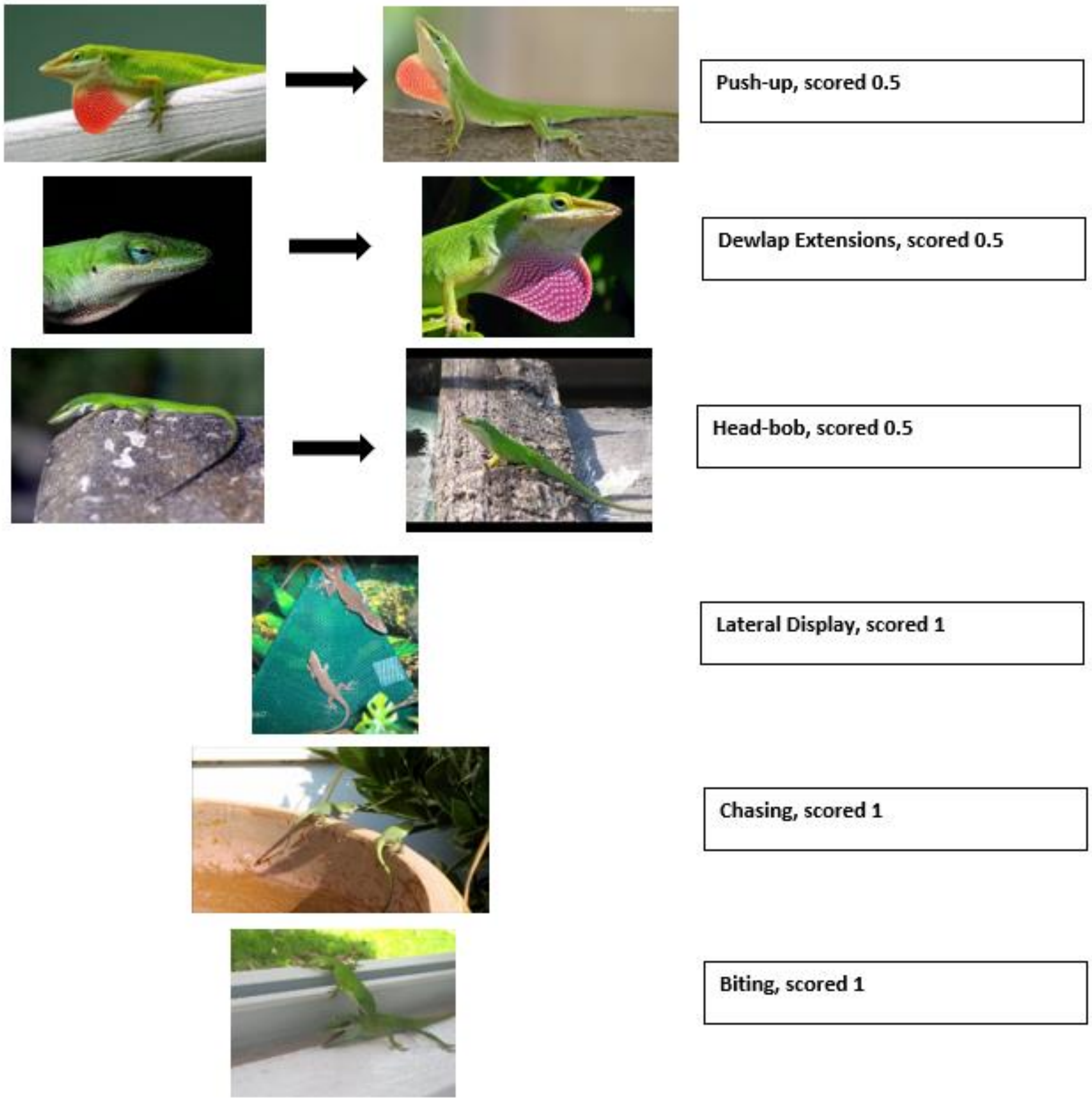


Figure 3. Depictions of aggressive actions used to score males during dyadic interactions.

Statistical Analyses

All statistical analyses were performed using SPSS (v25). All data, when possible, were logarithmically (Log_{10}) transformed to achieve normality. To determine whether there were relationships between dewlap size, body size, maximum bite force, relative latency, and absolute latency, I performed a Pearson correlation between each pairing. To determine if there were significant differences between the winners and losers of the dyadic interactions in terms of their dewlap size, mean bite force, maximum bite force, and absolute latency, I performed a Mann-Whitney U test for each variable as I could not achieve normality for these data. I used linear regression to test for predictive relationships between dewlap size and mean bite force, dewlap size and maximum bite force, dewlap size and latency to bite, SVL and mean bite force, SVL and maximum bite force, and SVL and latency to bite. To test for differences in latency to bite based on body size, lizards were divided into quartiles based on snout-vent length and latency to bite was examined using an ANOVA. All results were considered significant at $p<0.5$.

Results

I found no significant difference in the size of the dewlap between winners and losers of the dyadic interactions. Although dewlap signaling was utilized during 10 out of 15 dyadic interactions, there was no difference in the size of the dewlaps between winners and losers, contrary to my prediction. The winners had a mean dewlap weight of 0.00764g (se=0.001403) and the losers had a mean dewlap weight of 0.005545g (se=0.0005455). A Mann-Whitney U test demonstrated that the dewlaps were not significantly different in size (Mann-Whitney U=50.500, n=22, p=0.519, Figure 4).

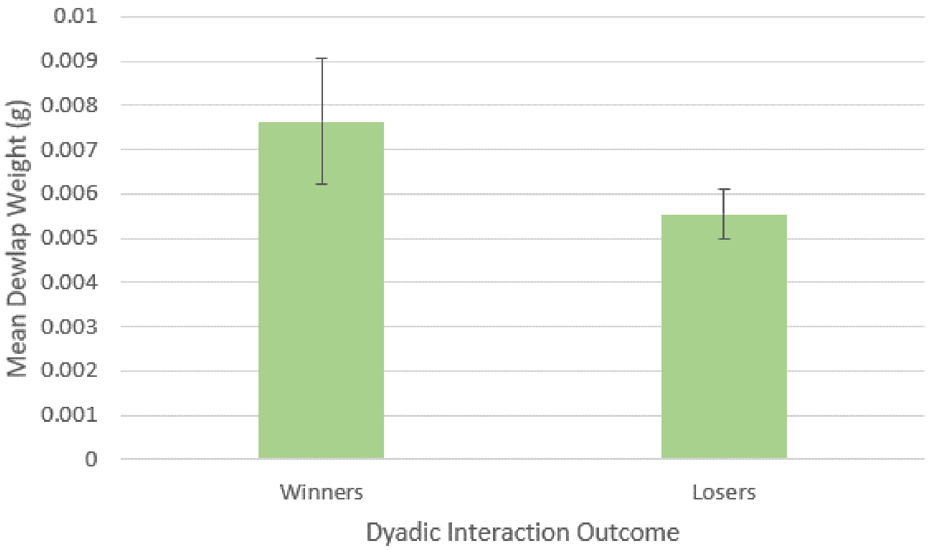


Figure 4. Mean dewlap weight of winners and losers of dyadic interactions. The weights were not significantly different. Bars represent the standard error.

I found no significant difference in mean bite force between winners and losers of the dyadic interactions. This is contrary to my prediction, as I would expect that winners of the dyadic interactions would have a stronger bite force than losers. Winners had a mean bite force of 45.7391g (se=8.73882) and losers had a mean bite force of 34.4827g (se=5.44282). A Mann-Whitney U test demonstrated that the mean bite forces were not significantly different (Mann-Whitney U=47.500, n=22 p=0.401, Figure 5).

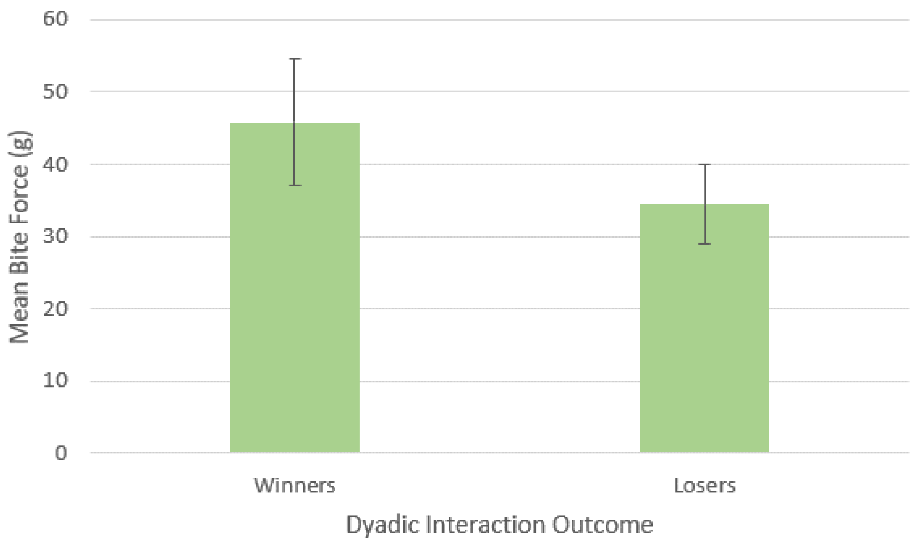


Figure 5. Mean bite force of winners and losers of dyadic interactions. Mean bite forces were not significantly different. Bars represent the standard error.

I found no significant difference in maximum bite force between winners and losers of the dyadic interactions. This is contrary to my predictions, as I would expect winners of the dyadic interactions to have a stronger maximum bite force than losers. Winners had a mean maximum bite force of 83.2273g (se=19.40047) and losers had a mean maximum bite force of 68.7636g (se=11.35115). A Mann-Whitney U test demonstrated that the maximum bite forces were not significantly different (Mann-Whitney U=62.500, n=22, p=0.898, Figure 6).

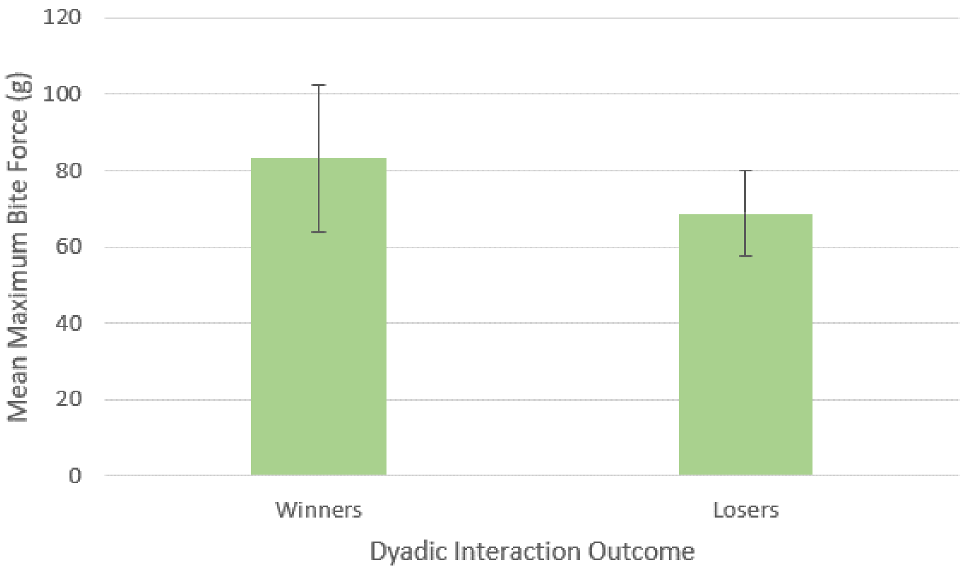


Figure 6. Mean maximum bite force of winners and losers of dyadic interactions. Mean maximum bite forces were not significantly different. Bars represent standard error.

I found a significant relationship between a male's dewlap size and his snout vent length (Simple Regression, R=0.589, R^2=0.346, F=18.025, df=1,35, p=0.000, Figure 7). This is what I expected, as the size of a male's dewlap is correlated with his body size. Males with larger snout vent lengths have larger dewlaps.

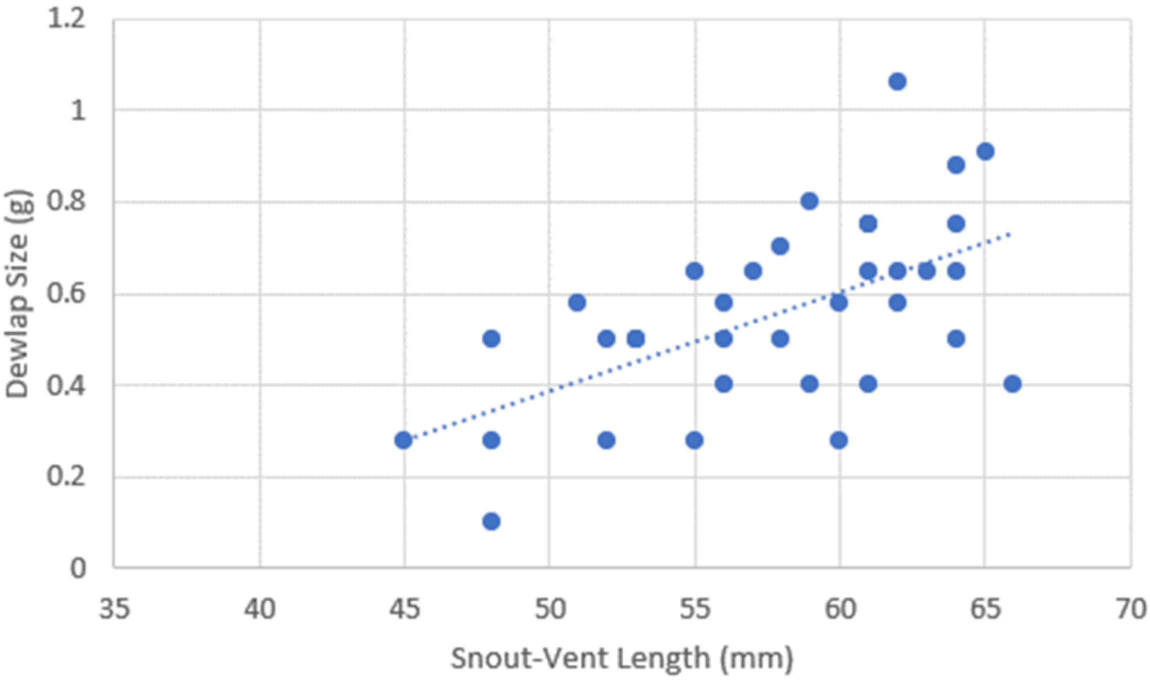


Figure 7. Linear regression showing a significant relationship between a male's dewlap size and his snout-vent length. Data for dewlap weights were transformed using a Log_{10}+2.8 transformation to achieve normality.

I found a significant relationship between a male's dewlap size and his mean bite force (Simple Regression, R=0.430, R^2=0.185, F=7.708, df=1,35, p=0.009, Figure 8). Males with larger dewlaps tend to have a stronger mean bite.

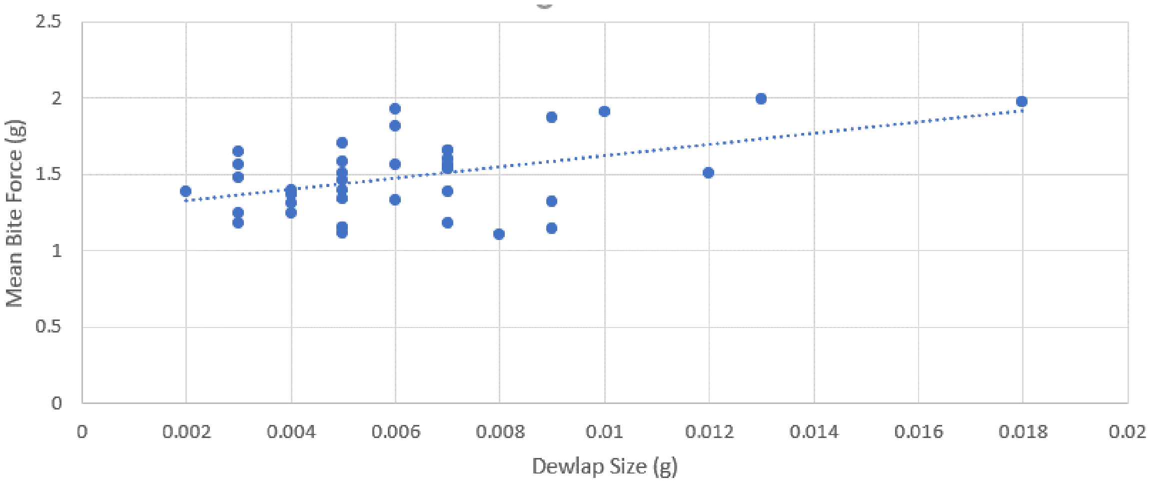


Figure 8. Linear regression showing a significant relationship between a male's dewlap size and his mean bite force. Data for mean bite force was transformed using a Log_{10} to achieve normality.

I found a significant relationship between a male's dewlap size and his maximum bite force (Simple Regression, R=0.424, R^2=0.179, F=7.435, df=1,35, p=0.010, Figure 9). Males with larger dewlaps tend to have a stronger maximum bite.

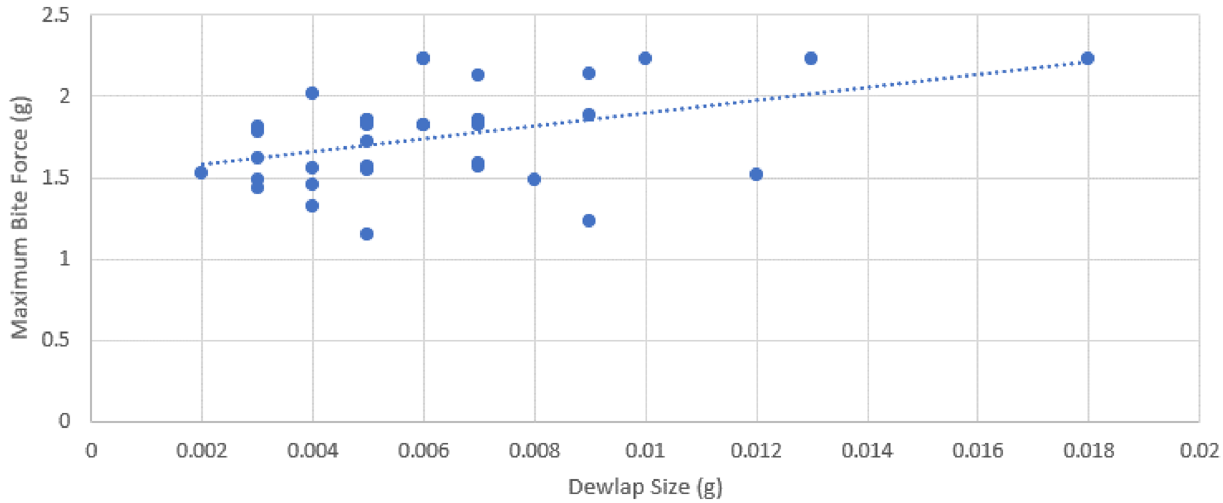


Figure 9. Linear regression showing a significant relationship between a male's dewlap size and his maximum bite force. Data for maximum bite force was transformed using a Log_{10} transformation to achieve normality.

There was a significant difference in the absolute latency to bite between winners and losers of the dyadic interactions. Winners had a mean absolute latency more than twice that of losers (winners: 57.6818s [se=10.89668]; losers: 26.9091s [se=7.25942]). The Mann-Whitney U test demonstrated that winners waited significantly longer to bite than did the losers (Mann-Whitney U=24.000, n=22, p=0.016, Figure 10).

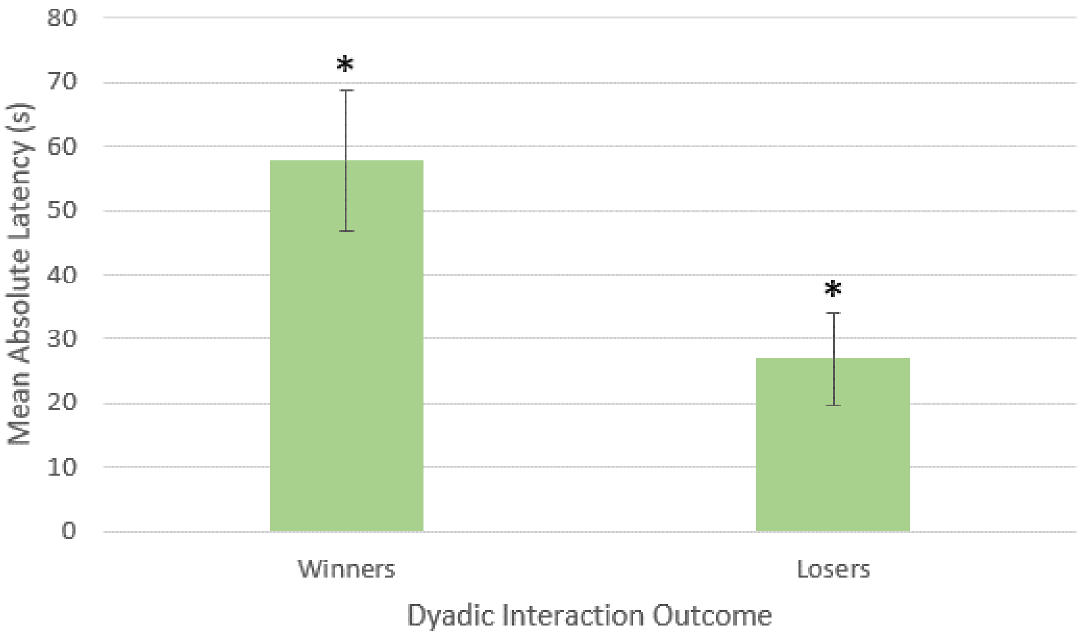


Figure 10. Mean latency to bite of winners and losers of dyadic interactions. Winners waited a significantly longer time to bite than losers. Bars represent standard error.

I found a significant relationship between a male's dewlap size and his absolute latency to bite (Simple Regression, R=0.397, R^2=0.157, F=6.350, df=1,35, p=0.017, Figure 11). Males with larger dewlaps tended to wait longer to bite.

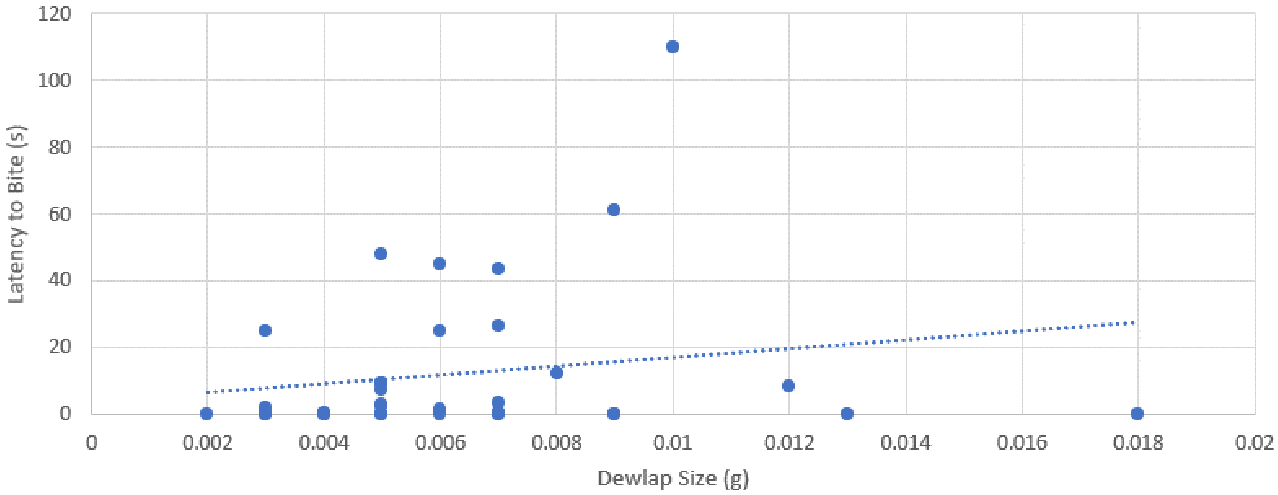


Figure 11. Linear regression showing a significant relationship between a male's dewlap size and his absolute latency to bite.

Discussion

Based on my results summarized in Table 2, I found four primary outcomes. First, there was no significant difference in the sizes of the dewlaps between winners and losers of dyadic interactions. Because the males were paired for body size, this suggests that the size of the dewlap itself does not predict the winner of a combat. Second, I found no significant difference in either the mean bite force or the maximum bite force between winners and losers of the dyadic interactions. This suggests that bite force does not act as a predictor for the winner of the combats. Third, I found that the size of a male’s dewlap predicts his mean and maximum bite forces. Fourth, I found that the size of a male’s dewlap does predict his latency to bite; winners of dyadic interactions tended to wait significantly longer to bite than losers did. These results suggest that, while I found no morphological traits that act as predictors for winning a dyadic interaction, the dewlap may predict behavioral characteristics that can be used to gauge an individual’s fighting capabilities.

Is there a significant difference in the size of the dewlap between winners and losers of dyadic interactions?	No
Is there a significant difference in mean bite force between winners and losers of dyadic interactions?	No
Is there a significant difference in maximum bite force between winners and losers of dyadic interactions?	No
Is there a significant relationship between a male’s dewlap size and his snout vent length?	Yes
Is there a significant relationship between a male’s dewlap size and his mean bite force?	Yes
Is there a significant relationship between a male’s dewlap size and his maximum bite force?	Yes
Is there a significant difference in the absolute latency to bite between winners and losers of dyadic interactions?	Yes
Is there a significant relationship between a male’s dewlap size and his absolute latency to bite?	Yes

Table 2. Summary of main findings.

In many animal species, particular features are used to display honest signals of an individual’s aggressiveness, and, in turn, the potential for winning aggressive encounters (Andersson 1994). By correlating with the animal’s likelihood of winning a fight, they serve the same function as a physical attack in terms of intimidating opponents and winning contests, thereby making them an important part of aggressive interactions (van Staaden et al. 2011). Animals utilize honest signals from their opponents when traits such as body size or relative strength are hard to quickly assess, making honest signals important for individuals to avoid potentially costly fights. For instance, in a study of wild-caught European green lizard (*Lacerta viridis),* males utilize UV reflectance on their throat patches to honestly signal their fighting abilities; in 88 percent of experimental trials, males with less UV reflectance than their opponent retreated from an aggressive encounter, avoiding a fight based on the signal from their opponent (Bajer et al. 2011).

Dewlap extension is a core feature of aggressive display behaviors in *A. carolinensis*, and is especially utilized by males during invasion of their established territory by another male (Jenssen 1977). In fact, the dewlap is one of the first signals used by males during aggressive encounters, prior to other signaling such as head-bobs or push-ups (Jenssen 1977). My results were consistent with those of Henningsen and Irschick (2012) who found that dewlap size in male *A. carolinensis* was correlated with an individual's maximum bite force. Additionally, male lizards with a stronger bite force tend to be the victors in staged combats, even when matched for body size (Husak et al. 2006). Considering that the dewlap is a prominent feature of the green anole signal repertoire, a male with a larger dewlap has a stronger bite force, and males with a stronger bite force tend to be the victors of staged combats, the dewlap itself could be considered an honest signal of aggressive capacity and the likelihood of winning a combat.

My results, however, do not support this hypothesis, as males with larger dewlaps were not significantly more likely to win a dyadic interaction. In addition, the size of a winner's dewlap did not predict his mean or maximum bite force, contrary to what other researchers have reported (Vanhooydonck et al. 2005). In fact, the situation was more complex and interesting. I found that although dewlap size did not directly predict the winner's likelihood to bite or his mean or maximum bite forces, males with larger dewlaps have a longer latency to bite and have stronger mean and maximum bite forces than do males with smaller dewlaps.

When the winners of dyadic interactions were divided into quartiles based on their snout-vent lengths, I found no difference in their latency to bite, suggesting that an individual's size does not predict how long it takes until his initial bite. However, considering that dewlap displays were used in eight of the thirteen dyadic interactions, a male is likely to be using his dewlap to convey some information about himself to his opponent. Knowing the dewlap is used to display traits such as the male's species, sex, and perhaps his individual identity, I cannot discount these as possibilities for what the male is signaling. However, because individuals were matched for body size during the dyadic interactions, and body size does not predict their latency to bite, the dewlap could be utilized for something else in addition to signaling body size.

A potential explanation for why my results contradict previous literature (Jenssen 1997; Husak et al. 2006; Vanhooydonck et al. 2005) could be due to experimental constraints. In previous studies on *A. carolinensis*, Jenssen et al. (2004) utilized wild caught adult males. Due to time and resource constraints, I utilized purchased *A. carolinensis* rather than wild caught. I cannot be certain how the lizards were raised prior to my purchasing them. It is possible they were raised in captivity, potentially altering their aggressive behaviors compared to males who are wild caught. However, according to Carolina Biological Supply, the lizards they sell are wild-caught, although we still cannot be certain how long they have lived in captivity. Additionally, other studies were able to give their males in the interaction tank a longer acclimation period. Jenssen

(1997) and Forster et al. (2004) utilized a week-long acclimation period, a time frame double what I was able to provide due to time limitations as a result of COVID-19 restrictions. My shortened acclimation period could have affected the outcome, as the males did not have enough time to become territorial or possessive of their respective females as the animals in the cited studies. These factors, however, would not have affected my lizards' dewlap sizes or bite forces, and although my animals may have been raised in captivity, they should still maintain their fundamental aggressive behaviors in adulthood.

Another potential explanation for my contradictory results is the different personalities of individual male *A. carolinensis.* Animal personality is the repeatable individual differences in behavior, influencing how an individual interacts with the environment, mates, predators, and competitors (Roche et al. 2016). Although this is a relatively new area of inquiry, over the last two decades literature has increasingly provided support for the concept of animal personality (as reviewed in Bolnick et al. 2003; Dall et al. 2004; Reale et al. 2007). The focus of animal personality research involves how individuals of a species behave in relation to one another, not the absolute behavior expressed by an individual, allowing researchers to compare the different responses of individuals of the same species in the same situation (Stamps and Groothuis 2010). Animal personality can change what specific behavior an individual expresses in a given situation; this ability can vary widely among individuals of the same species in the same situation (Stamps and Groothuis 2012). Stamps and Krishnan (2014) suggest that these differences arise during ontogeny; even individuals raised under the same conditions can express different personality traits as adults. Evidence of animal personality is now widespread and has been documented in ants, fishes, crustaceans, birds, lizards, rodents, and several species of mammal (Nilsson et al. 2014; Stamps and Groothuis 2012).

The term “personality”, as generally applied to humans, encompasses characteristics of an individual including its disposition, goals, moods, and attitudes, implying the need for underlying emotional processes (Pervin 2008). To eliminate such anthropomorphic characteristics when studying animals, researchers focus on a subset of these characteristics termed personality “traits”. Personality trait research deals with the way an individual reacts in particular situations or at particular times, providing measurable characteristics that do not rely on underlying cognition (Pervin 2008). In order to provide measurable characteristics for studying animal personality, Reale et al. (2007) suggested dividing behaviors into five categories that can all be quantified based on an individual’s actions: boldness, activity, exploration, sociability, and aggression.

Boldness, or the propensity of individuals to take risks, is one of the most commonly measured personality traits, and can be used to test an animal’s response to a novel environment, risk of predation, or within-species combat (Carter et al. 2012). Understanding this leads one to suspect that the size of the dewlap could be used as a signal of a male’s boldness, in turn presenting information to an opponent about his propensity to persist in combat. Studies involving crickets, lizards, and rainbow fish indicate that personality can influence the outcome of aggressive interactions when there is no difference in the sizes of the individuals, suggesting boldness plays a role in determining the winner (Arnott and Elwood 2009; Santostefano et al. 2016; Colleter and Brown 2011). For example, in laboratory-reared European green lizards (*Lacerta viridis)*, individuals express differences in personality traits, specifically in regard to their boldness and their willingness to take risks (Bajer et al. 2015). Although all males were raised in the same laboratory conditions, some males were more likely to explore a novel habitat (even in the presence of predators) than others, suggesting individual differences in personality among males (Bajer et al. 2015). Some lizards appeared to be bolder, while other appeared to be more cautious. From these studies, we can hypothesize that a male *A. carolinensis* may use his dewlap as a signal of his overall caution: although males with larger dewlaps have stronger bite forces, they may not be willing to enter into combat immediately.

Lizards with larger dewlaps, who have stronger bite forces, tend to wait longer to bite in combat situations, potentially exhibiting they are cautious. The development of bold and cautious males may be explained by the way natural selection has shaped behavioral traits in *A. carolinensis.* In order for a behavior to persist, the benefits of said behavior must outweigh the costs associated with it. Aggressive interactions, whether to ward off predators or during intraspecies combat, increase the energy the animal must expend, reduce the time to forage for food or to find potential mates, and come with the risk of injury or death to both winners and losers. Additionally, male green anoles who are more aggressive are potentially more susceptible to predation and require more energy to maintain their bold lifestyle (Borgsman et al. 2020).

However, being bold can also provide evolutionary advantages. Although boldness may increase an individual's risk of predation, being bold may also increase an individual's productivity and reproductive success. In several species, including the fishing spider (*Dolomedes spp.)*, Japanese quail (*Coturnix japonica)*, domestic chicken *(Gallus gallus domesticus),* Atlantic silverside (*Menidia menidia)*, stickleback *(Gasterosteidae spp.)*, rainbow trout *(Oncorhynchus mykiss)*, domestic pig *(Sus scrofa domesticus),* and bighorn sheep *(Ovis canadensis)*, increased boldness is associated with an increase in food intake, growth, and fecundity (Biro and Stamps 2008). This increase in productivity and reproductive success may result from a correlation between boldness and other personality traits, including exploration. As Borgsman and colleagues (2020) found for green anoles, bolder individuals tend to spend more time exploring their environment rather than hiding from predators, increasing the amount of food as well as the number of potential mates they are able to obtain. For *Anolis carolinensis,* males who express bolder behavioral traits may be more likely to explore their environment, procure food, and mate with more females than males who exhibit fewer exploratory behaviors. This is especially important considering their restrained mating season, as the males have a limited window to procure mates.

Research on *Anolis sagrei* found that when no predators were in their vicinity, males were less likely to express aggressive behaviors, even in the presence of a competitor (Lapiedra et al. 2018). Instead, the males were more focused on exploratory rather than aggressive behaviors. In my experimental trials, the lizards may have been showing more caution than boldness in response to their new environment. When no obvious predators (such as snakes, birds, or small mammals) are present that must be immediately avoided, it may be more energetically efficient to avoid combat, reducing both energy expenditure and the risk of injury.

Other studies have found that *A. carolinensis* prefers to utilize signaling or retreating rather than physical displays of aggression, and only resorts to physical combat if neither lizard retreats (Culbertson and Herrmann 2019). The large dewlap of an aggressor could signal to his opponent that he has a stronger bite force, giving him a higher chance of winning in physical combat if one were to occur. His bite force, however, does not mean there is no chance of serious physical injury or death if a fight were to occur. By displaying his large dewlap, he could be signaling to his combatant that he has a high chance of winning, therefore possibly avoiding a fight altogether and providing an overall energetic advantage to both individuals.

As with other honest signals used by animals, there is the potential that male *A. carolinensis* adults could have a large dewlap that does not correlate with their bite force or aggressiveness. It would seem beneficial for a smaller, less aggressive male to exhibit a large dewlap to deter opponents and prevent combat. However, if the dewlap itself is energetically costly to produce or maintain, it may have significant physiological costs to the individual. Lailvaux et al. (2000) found that *A. carolinensis* males raised in nutrient-deprived environments had smaller snout-vent lengths and reduced bite forces than those raised in normal conditions. In a situation where a male is faced with nutritional constraints, more energy will need to be focused on traits that increase his ability to obtain food, such as maintaining a strong bite force. Utilizing energy for the maintenance of a large dewlap is potentially costly, as this energy could be better spent increasing an individual's bite force to increase food procurement.

Another potential aspect regarding the size of a male's dewlap is its multiple uses. The dewlap is known to be involved not only in male-male combat, but also in female mate choice, and in species recognition (Jenssen et al. 2000). While having a large dewlap may be beneficial in male-male combat, it may render the bearer more susceptible to predators (Andersson 1994). The dewlaps of five different *Anolis* species, including *A. carolinensis*, have been found to contain UV reflective patches, which increase in number as the dewlap size increases (Fleishman et al. 1993). Researchers have found that this reflectance may play an important role in visual signaling involved in sexual selection by a female, as female *A. carolinensis* seem to be attracted to both the basic red color and the UV reflectance of the dewlap (Crews 1975). While again, this would seem to point to an advantage for a male having a larger dewlap, other animals, including some predators, are also able to see this UV reflectance.

Experiments on the reflectance of the bands on bluethroat's (*Luscinia svecica)* legs found that females showed preferences for different males based on the amount of UV reflectance (Fiske and Amundsen 1997). While that experiment focused on the importance of UV on sexual selection in birds, it provides evidence that birds are, in fact, able to see UV reflectance. A male anole who presents a large dewlap may be able to increase his number of potential mates and ward off potential combats, however he is potentially making himself easier to spot by predators. Such predator-prey interactions are important for the development of a signal, as signals that become too prominent expose an individual to increased predation. Therefore, the size of the dewlap in male *A. carolinensis* is most likely influenced by a combination of predation and sexual selection, producing a limit on how large the dewlap grows and why it may be unfavorable to utilize the dewlap as a dishonest signal.

My study provides insight into potential unexplored uses of the dewlap in the male green anoles. Although my results contradicted some previous research, the dewlap is still an integral part of the signaling repertoire during male-male combat. The possible use of the dewlap to signal the cautiousness of the individual provides new avenues for the studies of animal personality. Future work should concentrate on elucidating more nuances regarding animal personality, with the green anole a potential candidate for this research.

Literature Cited

Andersson M. 1994. Sexual Selection. Princeton (NJ): Princeton University Press.

Andersson M and Simmons LW. 2006. Sexual selection and mate choice. Trends in Ecology and Evolution. 21(6): 296-302.

Arnott G, Elwood RW. 2009. Assessment of fighting ability in animal contests. Animal Behavior. 77: (991-1004).

Bajer K, Horvath G, Molnar O, Torok J, Garamszegi LZ, Herczeg G. 2015. European green lizard (*Lacerta viridis)* personalities: linking behavioural types to ecologically relevant traits at different ontogenetic stages. Behavioural Processes. 111: 67-74.

Bajer K, Molnar O, Torok J, Herczeg G. 2011. Ultraviolet nuptial colour determines fight success in male European green lizards (*Lacerta viridis).* Biology Letters. 7(1): 866-868.

Biro PA, Stamps JA. 2008. Are animal personality traits linked to life-history productivity? Trends in Ecology and Evolution. 23(7): 361-368.

Bloch N and Irschick DJ. 2005. An analysis of inter-population divergence in visual display behavior of the green anole lizard (*Anolis carolinensis).* Ethology. 112(1): 370-378.

Bolnick DI, Svanback R, Fordyce JA, Yang LH, Davis JM, Hulsey CD, Forister ML. 2003. The ecology of individuals: incidence and implications of individual specialization. The American Naturalist. DOI: https://doi.org/10.1086/343878

Borgmans G, Van den Panhuyzen S, Van Damme R. 2020. The (dis)advantages of dominance in a multiple male group of *Anolis carolinensis* lizards. Zoology. 139: 125-137.

Candolin U. 2000. Male-male competition ensures honest signaling of male parental ability in the three-spined stickleback (*Gasterosteus aculeatus).* Behavioral Ecology Sociobiology. 49(1): 57-61.

Carter AJ, Feeney WE, Marshall HH, Cowlishaw G, Heinsohn R. 2012. Animal personality: what are behavioural ecologists measuring? Biological Reviews. 88(2): 465-475.

Colleter M and Brown C. 2011. Personality traits predict hierarchy rank in male rainbow fish social groups. Animal Behaviour. 81(6): 1231-1237.

Conant R and Collins JT. 1991. Reptiles and amphibians of Eastern/Central North America (Peterson Field Guides). Houghton Mifflin Company. p 90.

Crews D. 1975. Effects of different components of male courtship behaviour on environmentally induced ovarian recrudescence and mating preferences in the lizard, *Anolis carolinensis.* Animal Behavior. 23(1): 349-356.

Culbertson KA, Herrmann NC. 2019. Asymmetric interference competition and niche partitioning between native and invasive *Anolis* lizards. Oecologia. 190(4): 811-820.

Dall SR, Houston AI, McNamara JM. 2004. The behavioural ecology of personality: consistent individual differences from an adaptive perspective. Ecology Letters. 7(8): 734-739.

Dawkins R and Krebs JR. 2004. Animal signals: information or manipulation? In: Smith JM and Harper D, editors. Animal signals. Oxford (UK): Oxford University Press. p. 282-309.

Deperno CS and Cooper WE. 1994. Strike-induced chemosensory searching is absent in *Anolis carolinensis.* Amphibia-Reptilia. 15(1): 83-88.

Driessens T, Vanhooydonck B, Van Damme R. 2014. Deterring predators, daunting opponents or drawing partners? Signaling rates across diverse contexts in the lizard *Anolis sagrei.* Behavioral Ecology Sociobiology. 68(1): 173-184.

Emlen DJ. 2008. The evolution of animal weapons. Annual Review of Ecology, Evolution, and Systematics. 39(1): 387-413.

Fiske P and Amundsen T. 1997. Female bluethroats prefer males with symmetric colour bands. Animal Behavior. 54(1): 81-87.

Fleishman LJ. 1992. The influence of the sensory system and the environment on motion patterns in the visual displays of anoline lizards and other vertebrates. American Naturalist. 139(1): 36-61.

Fleishman LJ, Loew ER, and Leal M. 1993. Ultraviolet vision in lizards. Nature. 365(1): 397.

Greenberg N. 1977. A neuroethological study of display behavior in the lizard *Anolis carolinensis* (Reptilia, Lacertilia, Iguanidae). American Zoology. 17(1): 191-201.

Greenberg R and Noble GK. 1994. Social behavior of the American chameleon *(Anolis carolinensis* Voigt). Physical Zoology. 17(1): 392-439.

Henningsen JP, Irschick DJ. 2012. An experimental test of the effect of signal size and performance capacity on dominance on the green anole lizard. Functional Ecology. 26: 3-10.

Herrel A, Spithoven L, Van Damme R, De Vree F. 1999. Sexual dimorphism of head size in *Gallotia galloti:* testing the niche divergence hypothesis by functional analyses. Functional Ecology. 13(1): 289-297.

Husak JF, Lappin AK, Fox ST, Lemos-Espinal JA. 2006. Bite-force performance predicts dominance in male venerable collared lizards (*Crotaphytus antiquus).* Copeia. 2006(2): 301-306.

Jenssen TA. 1977. Evolution of anoline lizard display behavior. American Zoology. 17: 203-215.

Jenssen TA, Greenberg N, Hovde KA. 1995. Behavioral profile of free-ranging male lizards, *Anolis carolinensis,* across breeding and post-breeding seasons. Herpetological Monographs. 9(1): 41-62.

Jenssen TA, Orrell KS, and Loven MB. 2000. Sexual dimorphism in aggressive signal structure and use by a polygynous lizard, *Anolis carolinensis.* Copeia. 1(1): 140-149.

Jenssen TA, Decourcy KR, Congdon JD. 2005. Assessment in contests of male lizards (*Anolis carolinensis*): how should smaller males respond when size matters? Animal Behavior. 69(6): 1325-1336.

Johnson MA and Wade. 2011. Chapter 2: Neuroendocrinology of reptilian reproductive behavior. Hormones and Reproduction of Vertebrates. 1(1): 39-61.

Kirkpatrick M. 1987. Sexual selection by female choice in polygynous animals. Annual Review of Ecology, Evolution, and Systematics. 18(1): 43-70.

Krebs JR and Davies NB. 1997. Behavioural Ecology. 4th edition. Hoboken (NJ): Wiley-Blackwell.

Lailvaux SP, Gilbert RL, Edwards JR. 2012. A performance-based cost to honest signaling in male green anole lizards (*Anolis carolinensis*). Proceedings of the Royal Society. 279(1): 2841-2848.

Lailvaux SP, Herrel A, Vanhooydonck B, Meyers JJ, Irschick DJ. 2004. Performance capacity, fighting tactics and the evolution of life-stage male morphs in the green anole lizard (*Anolis carolinensis).* Proceedings of the Royal Society. 271(1): 2501-2508.

Lapiedra O, Schoener TW, Leal M, Losos JB, Kolbe JJ. 2018. Predator-driven natural selection on risk-taking behavior in anole lizards. Science. 360(6392): 1017-1020.

Losos JB and Schneider CJ. 2009. *Anolis* lizards. Current Biology. 19(8): 316-318.

Lovern MB, Holmes MM, Wade J. 2004. The green anole (*Anolis carolinensis)*: a reptilian model for laboratory studies of reproductive morphology and behavior. ILAR Journal. 45(1): 54-64.

Medvin MB. 1990. Sex differences in coloration and optical signaling in the lizard *Anolis carolinensis* (Reptilia, Lacertilia, Iguanidae). Animal Behavior. 39(1): 192-193.

Nilsson J, Hansson L, Bronmark C, Chapman B. 2014. Individuality in movement: the role of animal personality. Chapter. DOI: 10.1093/acprof:oso/9780199677184.003.0006

Pentland A. 2010. Honest signals: how they shape our world. Cambridge (MA): MIT Press.

Perry G, Levering K, Girard I, Garland T. 2004. Locomotor performance and social dominance in male *Anolis cristatellus.* Animal Behaviour. 67(1): 37-47.

Pervin A. 2008. Handbook of Personality. New York (NY): The Guilford Press.

Reale D, Reader SM, Sol D, McDougall PT, Dingemanse NJ. 2007. Integrating animal temperament within ecology and evolution. Biological Reviews. DOI: https://doi.org/10.111/j.1469-185X.2007.00010.x

Roche DG, Careau V, Binning SA. 2016. Demystifying animal "personality" (or not): why individual variation matters to experimental biologists. Journal of Experimental Biology. 219: 3832-3843.

Searcy WA, Akcay C, Nowicki S, Beecher MD. 2014. Chapter three- aggressive signaling in song sparrows and other songbirds. Advances in the Study of Behavior. 46(1): 89-125.

Santostefano F, Wilson AJ, Araya-Ajoy YG, Dingemanse NJ. 2016. Interacting with the enemy: indirect effects of personality on conspecific aggression in crickets. Behavioral Ecology. 27(4): 1235-1246.

Setchell JM and Wickings EJ. 2005. Dominance, status signals, and coloration in male mandrills (*Mandrillus sphinx)*. Ethology. 111(1): 25-50.

Stamps J and Groothuis TGG. 2012. The development of animal personality: relevance, concepts and perspectives. Biological Reviews. 85(2): 301-325.

Stamps J and Krishnan VV. 2014. Individual differences in the potential and realized developmental plasticity of personality traits. Frontiers in Ecology and Evolution. DOI: https://doi.org/10.3389/fevo.2014.00069

Sullivan-Beckers L and Cocroft RB. 2010. The importance of female choice, male-male competition, and signal transmission as causes of selection in male mating signals. Evolution. 64(11): 3158-3171.

Tokarz RR. 1998. Mating pattern in the lizard *Anolis sagrei:* implications for mate choice and sperm competition. Herpetologica. 54(3): 388-394.

van Staadan MJ, Searcy WA, Hanlon RT. 2011. Signaling aggression. Advances in Genetics. 75(1): 23-49

Vanhooydonck B, Herrel AY, Van Dammes R, Irschick DJ. 2005a. Does dewlap size predict male bite performance in Jamaican *Anolis* lizards? Functional Ecology. 19: 38-42.

Vanhooydonck B, Herrel AY, Van Damme R, Meyers JJ, Irschick DJ. 2005b. The relationship between dewlap size and performance changes with age and sex in a green anole (*Anolis carolinensis)* lizard population. Behavioral Ecology Sociobiology. 59(1): 157-165.

Vortman Y, Lotem A, Dor R, Lovette IJ, Safran RJ. 2011. The sexual signals of the East-Mediterranean barn swallow: a different swallow tale. Behavioral Ecology. 22(6): 1344-1352.

Wagner WE. 1992. Deceptive or honest signaling of fighting ability? A test of alternative hypotheses for the function of changes in call dominant frequency by male cricket frogs. Animal Behaviour. 44(3): 449-462.

Williams EE and Rand AS. 1977. Species recognition, dewlap function and faunal size. American Zoology. 17(1): 261-270.

Wilson RS, Angilletta MJ, James RS, Navas C, Seebacher F. 2007. Dishonest signals of strength in male slender crayfish (*Cherax dispar)* during agnostic encounters. The American Naturalist. 170(2): 284-291.