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IMPORTANCE OF THE TAIL IN *ANOLIS CAROLINENSIS* FOR
CONTROLLING IN-AIR STABILITY

by

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A Paper Presented to the
Faculty of Mount Holyoke College in
Partial Fulfillment of the Requirements for
the Degree of Bachelors of Arts with
Honor

Program in Neuroscience and Behavior

South Hadley, MA 01075

May 2014

This paper was prepared
under the direction of
Professor Gary Gillis
for eight credits.

ACKNOWLEDGMENTS

I owe a great deal of thanks to Gary Gillis for his incredible support throughout this process and for sparking my interest in different areas of research. He provided countless edits and feedback for my writing and presentations. Somehow he also knew the exact times to push me, and the times instead to offer positive reinforcement.

I'd also like to acknowledge Sue Barry and Rachel Fink for their dedication to being a part of my thesis committee. They provided diverse opinions and were patient, welcome company within this process.

I extend obvious thanks to Thomas Liimatainen for his work in constructing the launch used in my project and also for his help in assessing anything that needed repair.

I want to thank Pam Matheson and Janelle Gagnon for extensive statistical support and guidance.

(Su)Zanne Cox was exceptionally helpful with statistics, figures, advice, and overall sanity.

I appreciate the support of all of the members of my lab for their hard work and encouragement: Jessica Murray, Nell Maynard, Ariela Schnyer, Mirialys Gallardo, and Erin Schikowski.

I would also like to thank Chi-yun Kuo for aid in the initial stages of my project.

I especially want to thank Curtis G. Smith for funding for this independent research.

Debbie Pietrowski and the entire staff of Mount Holyoke College Animal Care were indispensable in carrying for and answering questions about the lizards.

Additionally, I thank the Neuroscience and Behavior, Biology, and Psychology departments at Mount Holyoke College for supporting my work.

Lastly, it goes almost without saying that I am sincerely thankful for the encouragement I received from all of my friends and family.

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ABSTRACT

Anolis carolinensis, a species of arboreal lizard, relies on jumping as its principal form of locomotion. Previous studies suggest the importance of tail movements for stabilizing the body in mid-air in the pitch and roll axes. Caudal autotomy, the intentional self-severing of the tail, is common in these lizards in the wild as a self-defense strategy and means of escape from a predator's grasp. Given the role of the tail in stabilizing the flight phase of jumping, it is not surprising that a cost of caudal autotomy involves decreased in-flight body control during jumping.

I tested if green anoles use their tails to alter body movements in the yaw axis, by comparing tail movements between artificially destabilized animals at room temperature and cooled to $\sim 2^{\circ}\text{C}$ (where they are unable to actively move their tails). Additionally, I also studied whether lizards alter tail movement behavior after losing 75% of the tail. Results indicate that lizards do not move their tails actively to control for yaw instabilities nor do they modify tail movements following tail loss. This lack of an effect of temperature and behavioral modification suggest that movements of the tail are unimportant in minimizing angular displacements in the yaw plane.

INTRODUCTION

Green Anoles

The genus *Anolis* is in the family Polychrotidae, order Squamata, and class Reptilia. The genus contains over 300 species (Nicholson et al., 2005) and includes a wide variety of lizards collectively referred to as anoles. Anoles occupy a range of body sizes (33-191 mm), colors (green, brown, gray), and diets (variety of insects). They are found throughout Mexico, Central America and northern South America, as well as in the southeastern United States. They are perhaps best known for their radiation in the Caribbean Islands, where they have been categorized into six different ecomorphs (Figure 1). Ecomorphs are defined as different species that occupy similar environments and share similar appearance (e.g., color, size and relative tail length) and behavior (e.g., method of locomotion). Species within the same ecomorph are not necessarily related evolutionarily (Losos, 2009) and rather share similarities due to comparable selective pressures in the particular niches they inhabit.

For example, lizards in the trunk-crown ecomorph, which are arboreal and occupy branches, leaves and trunks of trees, are characterized by long tails, short-to-medium body lengths and frequent locomotion (Losos, 2009). *Anolis carolinensis*, or the green anole, is native to the Southeastern United States, intermediate in size (~2-6g), and is a good example of the trunk-crown ecomorph. *A. carolinensis* navigates through trees mainly by jumping (Losos & Irschick,

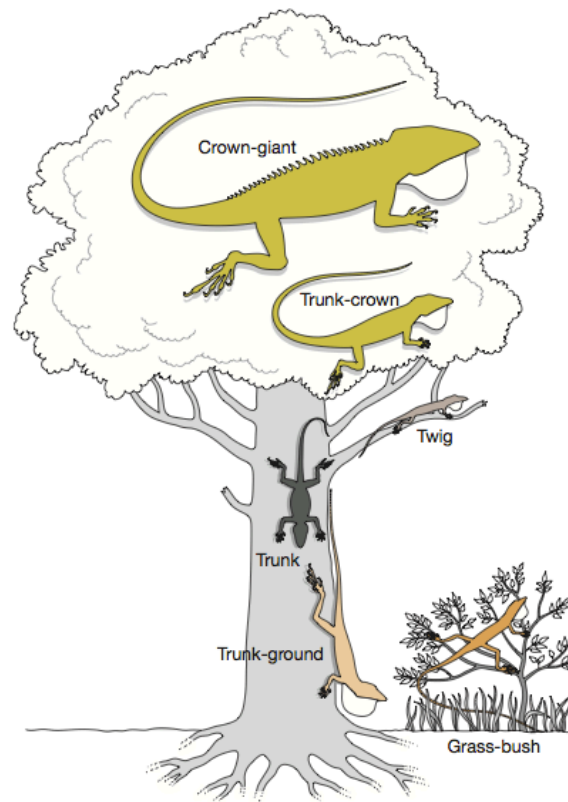


Figure 1. Anole ecomorphs. Each of the six ecomorphs occupies a different niche within the habitat. Some species prefer the tops of trees and others are typically found more in bushes (Losos, 2009).

1996; Irschick & Losos, 1998) and has been used in a variety of jumping studies (Bels et al., 1992; Lailvaux and Irschick, 2007, Toro et al., 2003).

Recently, work on in-air stability during lizard locomotion has established the importance of the tail during jumping or falling (Gillis et al., 2009; Jusufi et al., 2011). Such reliance on the tail seems to leave animals that have undergone caudal autotomy (tail loss) at a disadvantage with respect to correcting in-air instabilities.

Autotomy and its costs

Autotomy, in Greek “self-severing”, is the act of intentionally removing an appendage (or part of it) from the body, typically to escape a predator that has latched onto that appendage. It has been observed in snakes, starfish, insects, spiders, and lizards (Arnold, 1988; Klawinski & Formanowicz, 1994; Langkilde et al., 2005), and appendages that can be severed include arms, legs, or tails, depending on the species. Lizards perform caudal autotomy, or loss of the tail, and species within 13 of the approximately 20 lizard families are capable of voluntarily shedding the tail (Downes & Shine, 2001). Caudal autotomy is used as a self-defense strategy (Downes & Shine, 2001) and means of escape (Arnold, 1988). The release of the tail allows the lizard to escape the grasp of a predator and can serve as a distraction as it continues to writhe post-release, allowing the animal to flee.

Caudal autotomy only occurs at specific ‘breakage planes’ in the tail,

which are typically locations of structural weakness (Wilkie, 2001). The structural anatomy of these planes also allows for a clean breakage and supports reduced blood loss as well as fewer secondary, negative effects on neighboring tissues (Gilbert et al., 2013). Additionally, tissue damage at these locations triggers mechanical and chemical signaling that initiate direction of blood to the site for wound healing and inflammation limitation.

Apart from the benefits of self-defense and escape, there are several potential costs of caudal autotomy. Tail loss is coupled with loss of fat stores or energy reserves. Both male and female skinks, a type of lizard, use more fat stores from the tail than from other bodily fat stores to fuel reproductive activities (Smyth, 1974). A study of female geckos found that tailless females produced eggs with significantly lower energy content and overall mass than those of tailed females due to loss of caudal fat reserves (Dial & Fitzpatrick, 1981). A study by Clark (1971) found that some individuals of ground skink would return later to the site of autotomy and would eat the autotomized tail to regain the reserves.

There is also evidence for a decrease in male social status after autotomy. Fox & Rostker (1982) and Fox et al. (1990) demonstrated that loss of the tail in the lizard, *Uta stansburiana*, led to decreased dominance for the tailless male in male-male fights. Furthermore, Salvador et al. (1995) reported reduced home range areas, in addition to fewer females in those ranges, for males after tail loss.

There are costs associated with regeneration of the tail as well because individuals must reallocate resources to developing new tissues in order to rebuild

the tail, which negatively affects reproduction and/or growth (Maginnis, 2006). Additionally, once a section of the tail has been autotomized, it cannot be autotomized again distal to the original break point. The next severing can only occur closer to the body in a section that has never been autotomized.

Additional costs of autotomy include increased difficulty foraging and decreased survivorship. Fox & McCoy (2000) indicate that when lizards lost their tails they were more susceptible to predation than those with intact tails. Wilson (1992) also provides data demonstrating increased mortality after tail loss as a result of increased vulnerability to predators. Martín and Salvador (1993) reported shifts in microhabitats of tailless lizards to areas of decreased predation, however these areas contained fewer or less nutritious food sources. In another study, Downes and Shine (2001) presented a snake predator with inert, tailed and tailless lizards and the predator did not consume one more than the other. The results suggest that higher predation of tailless lizards may instead be due to a decrease in locomotor performance associated with autotomy rather than tail loss itself.

Locomotor costs of autotomy are linked with decreased performance in variables such as speed, endurance, climbing ability, and jump control and landing. Several studies on a variety of lizard species have shown that caudal autotomy leads to a decline in running speed (Downes & Shine, 2001; Chapple & Swain, 2002; Shine, 2003; Cooper et al., 2004) as well as reduced endurance (Bateman & Fleming, 2009). In addition, studies have shown a decrease in an arboreal lizard's ability to balance when climbing vertically since the tail acts as a

counterbalance to press against the substrate (Ballinger, 1973). Moreover, studies of lizard body control while in flight have focused on the importance of the tail for stabilizing the body.

Aerial control responses of the tail in arboreal lizards

Jumping and falling occur unpredictably in the natural world resulting in complex destabilizations, which in turn are presumably countered by complex tail movements. In the lab we are able to simplify destabilizations to almost a single plane in order to identify the nature of tail movements involved in responding to instabilities about a particular axis. Studies of the effects of tail loss on in-air stability have focused on pitch, rotation from front to back, and roll, rotation about an animal's longitudinal axis.

Caudal autotomy may negatively affect performance of aerial control as measured by body pitching during jumping. For example, a study by Bonvini (2007) demonstrated that caudal autotomy resulted in increased amounts of backwards pitching in *Anolis carolinensis*. Pre-autotomy jumps were characterized by consistent positive in-flight body angles with respect to the horizontal, but after tail loss, jumps of similar distances were characterized by a continuous increase in the body angle after takeoff. In other words, after takeoff, the subject pitched backwards throughout the aerial phase until landing. Bonvini also observed individuals that performed post-autotomy jumps in which they jumped down, directly toward the substrate, and thus maintained slightly negative

body angles (i.e., pointed downwards) with respect to the horizontal during the flight phase. This switch from consistently taking off with a positive body angle (i.e., oriented upward) to taking off with a negative body angle suggests that after autotomy some individuals might modify jumping behavior in order to achieve more stability in air and also more controlled landings.

Continuation of Bonvini's work by Gillis et al. (2009) measured the posterior body rotation in the jumps of green anole lizards before and after tail loss and found that tailed lizards rotated an average of only 5 degrees between takeoff and landing compared to an average of 30 degrees of rotation in tail-less animals (which sometimes rotated more than 90 degrees). Videos of lizards jumping with intact tails showed the lizards' tails dragged along the jumping surface during and shortly after takeoff, perhaps providing some stability as the animal entered the aerial phase of the jump. In autotomized lizards, there was no tail to perform this action, leading to the destabilized pitching movements observed after takeoff in these animals. Gillis et al. (2009) did note that after autotomy and during the aerial phase of a jump, as the animal pitched backwards, the tail stump appeared to be very active, undergoing many movements, suggesting the subject's attempts to use the tail to improve stability during flight and potentially to control pitching of the body.

Work on controlling rolling of the body in lizards was reported by Jusufi et al. (2008), who showed that the tail actively acts to right body orientation in falling geckos, *Cosymbotus platyurus*. When falling from an upside-down

position, tailed animals were significantly more successful than tail-less animals in righting their bodies. In free-fall, tailed animals moved the tail in a circular motion as they fell to rotate their bodies in the opposite direction prior to impact. Jusufi et al. (2011) studied aerial tail behaviors of a gecko, *Hemidactylus platyurus*, and an anole, *Anolis carolinensis*, and observed that the longer tail length of the anole compared to the gecko allowed for more effective body corrections in-flight. Despite the work devoted to the role of the tail in aerial body movement corrections for pitching and rolling, the actual, specific movements of the tail themselves have not yet been quantified since their isolation for study can be difficult.

In this study, I sought to study if and how lizards use their tails to correct for destabilization in the third axis of rotation, yaw, or rotation about the vertical axis. In particular I wanted to address three questions. First, do lizards use their tails to counteract instabilities about the yaw axis? Given that previous work has demonstrated the importance of the tail in helping animals correct for pitch (Gillis et al., 2009) and roll (Jusufi et al., 2008), I predicted that lizards would similarly employ tail movements to help them adjust movements about the yaw axis. Second, given the likely importance of tail movements for correcting yaw instabilities, I asked whether loss of part of the tail led to a change in the way an animal used this appendage. In other words, do animals change tail movement behavior after tail loss to compensate for the reduced appendage length? I predicted greater and faster movements of homologous tail points after partial

autotomy if animals were indeed attempting to behaviorally compensate for the loss in tail length. Finally, I asked whether lizards could adequately correct for in-air instabilities after autotomy (i.e., if they are compensating behaviorally, to what extent is it working, and if they're not, what, if anything, is the cost in terms of the outcome of the destabilization event?)

MATERIALS AND METHODS

Animals

Four green anoles (*Anolis carolinensis*) were used with a mean mass of 3.19 g, and a mean tail length of 10.7 cm. Animals were purchased from local pet stores and housed in glass tanks with branches, fake greenery, floor pads, and water bowls as well as a 40-60 watt light bulb. The tanks were kept in a temperature-controlled room (25 degrees Celsius) and underwent a 12-hour light-dark cycle. Females were housed all together and males were housed individually. Animals were fed a diet of crickets and mealworms. The Mount Holyoke College Institutional Animal Care and Use Committee approved all experiments.

The launch

The launch (Figure 2) was constructed at Mount Holyoke College by machinist Thomas Liimatainen. It has a metal base with a metal shaft connected to a Plexiglas platform that is 10.6 cm by 8.8 cm. A piece of black sandpaper was secured to the top of the platform to minimize any potential slipping of the animal when destabilized. A metal spring attached to the shaft was secured to maximize consistent rotation. To load the launch, I compressed the spring-element by pressing down on the platform and rotating it slightly clockwise until the pin matched up with the appropriate hole. The launch was released from the compressed state by pulling back on the lever, which removed the pin from

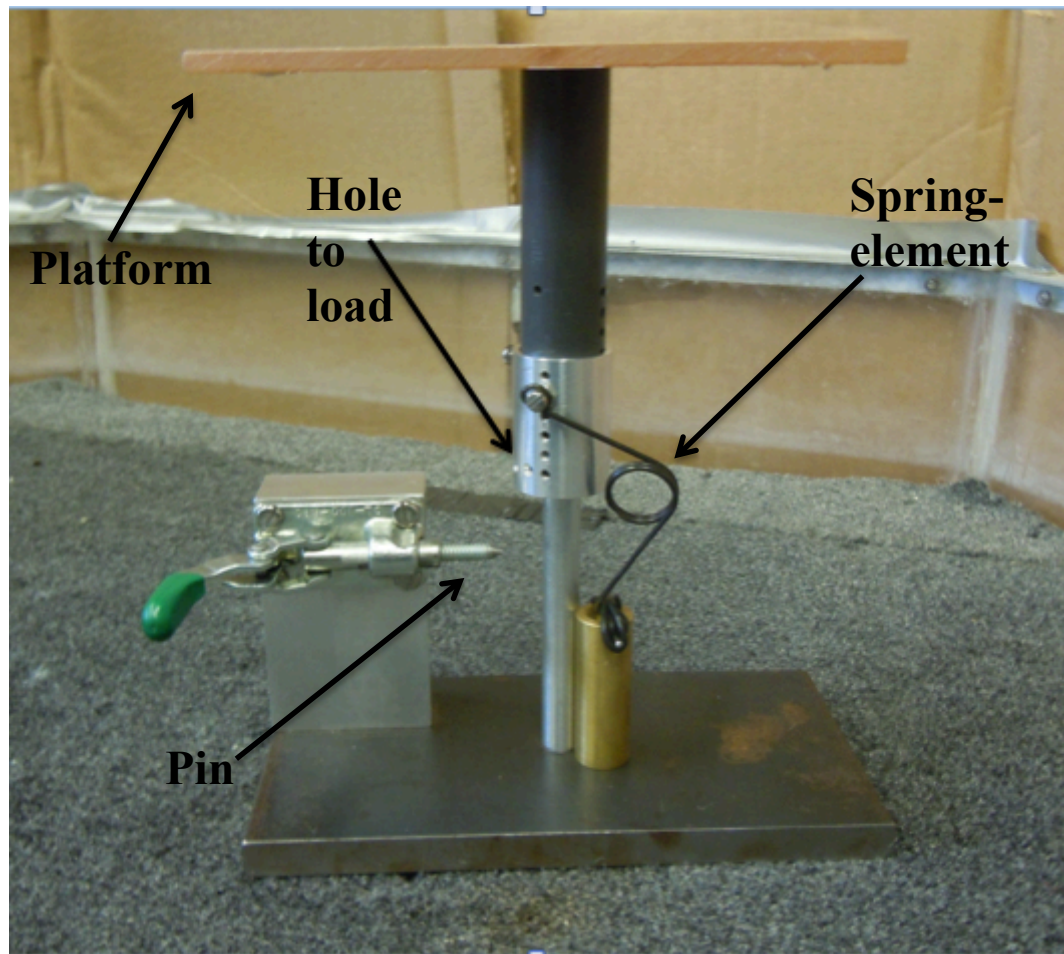


Figure 2. The destabilizing device. Three arrows indicate the platform, spring-element, and pin of the launch. The fourth arrow indicates the hole into which the pin was inserted to load the device.

the designated hole. This triggered the launch to move vertically one cm while simultaneously rotating ~90 degrees counter-clockwise, like a propeller.

Arena and camera set-up and video capture

We used an octagon-shaped arena, with a diameter of 1.52 m, constructed from a Plexiglas base covered in carpet and entirely surrounded by cardboard. Two 500W lights were used to illuminate the space. The launch was placed at the center of the arena in the same outlined location for all trials. Two Hi-Spec digital high-speed video cameras with a resolution of 1280 x 1024 pixels were pointed at the launch platform from orthogonal perspectives and oriented to capture the entire space of where each launch trial occurred. Using Hi-Spec software, the videos from each camera were captured at a rate of 506 frames per second and were saved together.

Pre-trials

For the first day of trials, each animal had a full tail and was individually weighed and its tail measured before being marked. To facilitate digitization, the animal was marked with White-Out or Liquid Paper using three lateral points on either side of the body (behind forelimb, middle (equidistant from the forelimb and hindlimb points), in front of hindlimb), three dorsal points aligned with the lateral points, three ventral points aligned with the lateral points, one on the tip of

the snout, and four rings evenly spaced down the tail at 25%, 50%, 75%, and the tip (Figure 3).

Trials and Conditions: Room temperature and cold, pre-autotomy and post-autotomy

I experimented with each animal through four different types of trials. On the first day, an animal underwent eight launches at room temperature with a full-length tail and no manipulation. Immediately afterwards, the animal was placed in the refrigerator for 20 minutes. This condition was intended to inhibit the animal's ability to make innate or voluntary movements of the tail and served as a control. Four trials were recorded with the same animal at the cold temperature and the animal was placed back in the refrigerator between launches. The following day, the tail was removed by grasping it with fine forceps at the 25% ring until the animal autotomized it. After 75% tail removal, animals were given five minutes to rest before beginning trials. I recorded eight launches for the autotomized tail trials at room temperature. Immediately afterwards, the animal was placed in the refrigerator for 20 minutes. Four trials were recorded with the same animal under the cold temperature and the animal was placed back in the refrigerator between launches.

Animals were always placed on the center of the platform in the same general orientation (Figure 3). Each animal was monitored and readjusted until it ceased movement and had achieved a desirable position with all four legs on

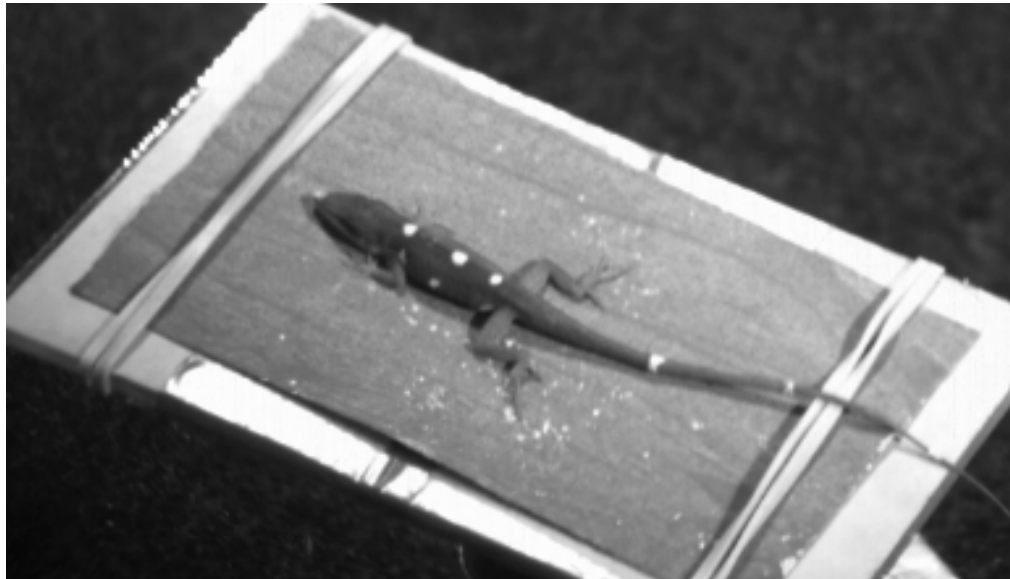


Figure 3. Point-marked subject positioned in the correct orientation on the platform before release.

the platform, its head in line with the body, a straight torso, and a straight tail projecting behind it. Once this condition was achieved, the launch was released. A trigger was used to stop the video recording.

Digitization

I randomly selected four videos from the original eight videos for each room temperature condition, so that each of the four conditions had an equal number of values to compare. I then digitized four videos per condition per subject, for a total of 16 videos per subject. Videos were digitized using MATLAB computer software, and I tracked four points in both camera views. One point was defined by the most anterior ring of points around the lizard's body and another by the most posterior ring of points on the lizard's body. A third point was digitized at the tip of the tail or at the 25% point, and the final point was digitized at the tip of the snout (Figure 4).

Statistical analysis

The independent variables were temperature (room temperature and cold) and autotomy (0% and 75%). The dependent variables were derived from measures of body and tail angles and velocities. From the videos of digitized body points, I calculated body rotation (yaw), landing body angle (torso), the angle between the head and body, and distance traveled by the tail tip and 25% point in the x, y, and z planes, in Microsoft Excel.

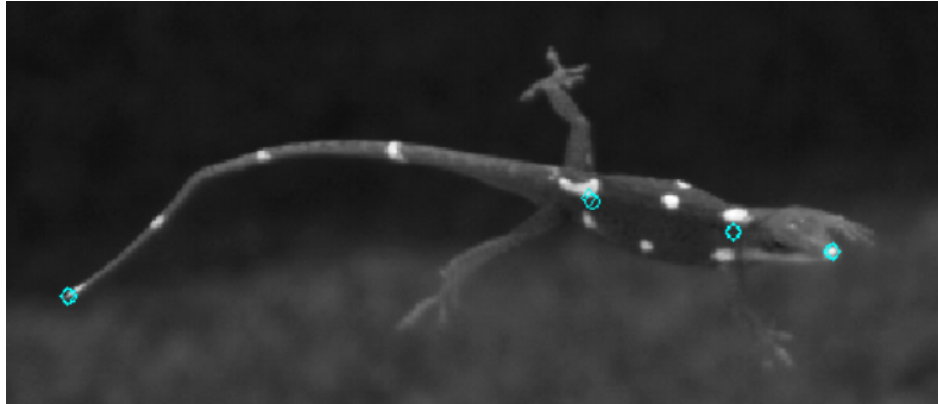


Figure 4. The four points digitized for one subject.

I used IBM SPSS Software to run paired-samples t-tests on the different variables between two sets of conditions: room temperature full tail vs. cold full tail and room temperature full tail vs. room temperature 25% tail. First, I assessed the typical distances traveled by the full tail in the room temperature and cold conditions. This was to address my first question of whether animals actually use specific tail movements to counteract destabilizations about the yaw axis. Then, I examined if there was a difference in the pre and post autotomy tail movements that could imply a shift in a lizard's behavior after autotomy (e.g. compensation for the lost length). Finally, I investigated variables such as motion and position of the lizards' body in the different condition comparisons to determine if there were any differences in coordination before and after tail loss.

RESULTS

Morphological measurements for each subject are represented in Table 1. Note that there is variability between subjects in the tail length pre-autotomy.

In every trial, regardless of condition, the subject was launched into the air with the same amount of force and was rotated counter-clockwise. On average, animals reached a height of about 20 cm at the apex of the launch before descending. Each trial, from release of the launch to first touchdown of the subject's body on the platform, was about 0.5 seconds long. Figure 5 depicts a three-dimensional color-representation of a subject at room temperature with its full tail. Note that the animal rotates counter-clockwise in the yaw plane. Also, note the tail movements from side to side on the up and down phases of the launch, as well as the circular tail movement at the apex of the launch. Across all the trials, when the tail was moved, it generally made similar kinds of directional movements. There were often circular rotations of the tail tip as well as movements made side to side in parallel with the subject's body.

First, the total distance traveled by the tip of the full tail at room temperature was compared to that traveled by the full tail tip in the cold condition. Although on average the tail tip moved farther in the warm condition, there was no significant difference between conditions (Warm: $M = 82.7$ cm, $SD = 41.0$ cm versus Cold: $M = 63.8$ cm, $SD = 10.5$ cm); $t(3) = 1.04$, $p = 0.38$ (Figure 6). The great variability in pre autotomy tail length (8.39 cm – 12.31 cm) contributed to

Table 1. Mass and tail length pre and post autotomy for four subjects.

Subject	Mass pre autotomy (g)	Mass post autotomy (g)	Tail length pre autotomy (cm)	Tail length post autotomy (cm)
Comet	2.19	2.14	8.39	2.10
Lucy	3.44	3.19	10.61	2.65
Persepolis	3.62	3.34	12.31	3.08
Shamrock	3.50	3.28	11.40	2.85

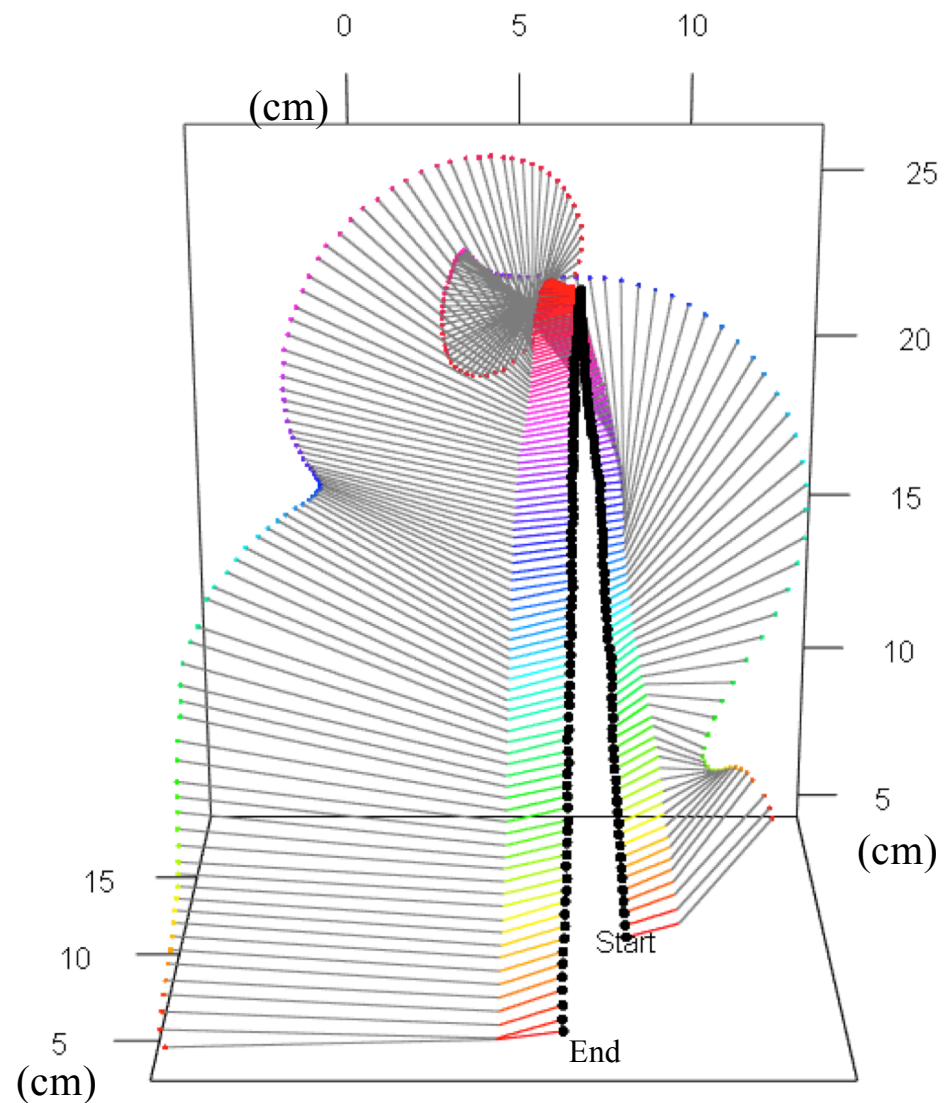


Figure 5. Three-dimensional color representation of the launch of one subject at room temperature with a full tail. The colored segment is the subject's body and the color cycles from red to pink through time from the initial position of the animal (marked by the word "Start") until landing (marked by the word "End"). The black dot represents the front end of the subject. The tip of the tail is also colored and is connected to the body segment by a gray line. Note the tail movements at the apex of the launch and during the up and down phases of the launch.

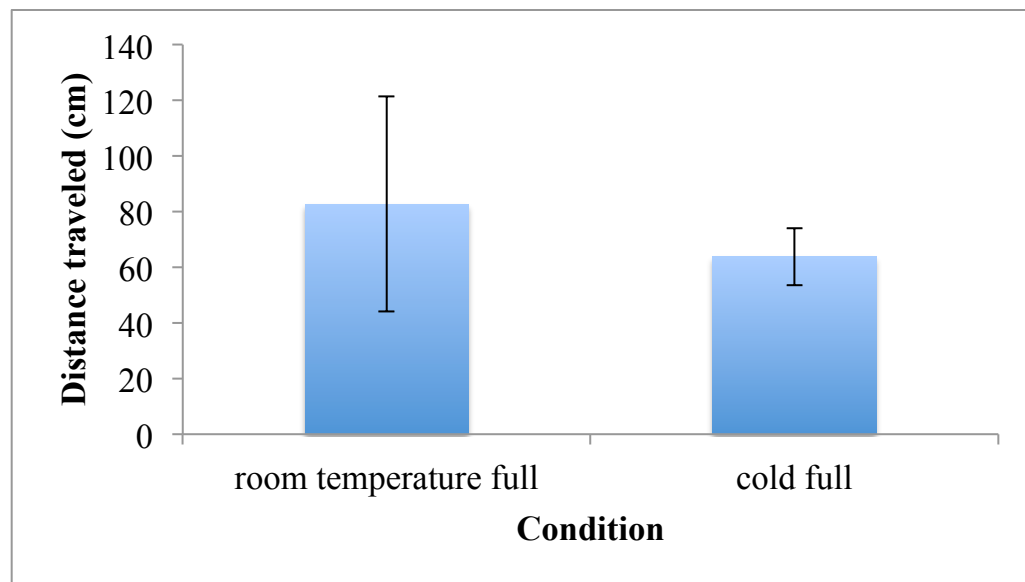
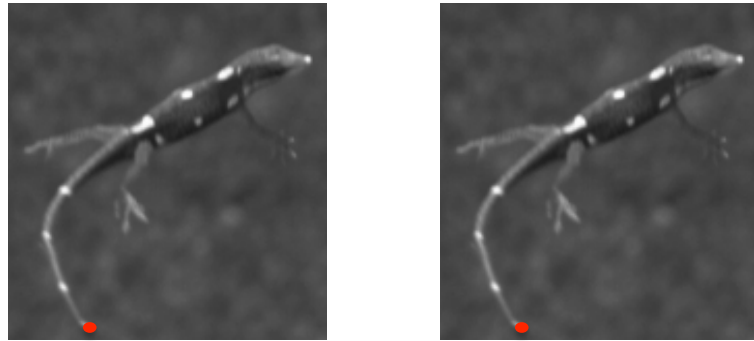


Figure 6. Mean distance traveled by the full tail tips in room temperature and cold conditions. The photos above the conditions represent the points that were digitized to collect data for this analysis. These data are from four subjects and four trials per subject for a total of 16 values per condition. There is no significant difference between conditions ($p = 0.38$).

the large standard deviation since, due to its length, the tip of a longer tail travels farther.

Next, the total distance traveled by the tip of the autotomized tail was compared with its homologous point on the full tail (the 25% point) at room temperature. Although on average the autotomized tail tip moved farther than the homologous point on the full tail, there was no significant difference between conditions (Autotomized tail: $M = 51.4$ cm, $SD = 7.41$ cm versus Full tail: $M = 45.2$ cm, $SD = 3.67$ cm); $t(3) = -1.83$, $p = 0.16$ (Figure 7).

To analyze animal body positions and motions that could be modified as a result of the tail loss, I compared the total amount of rotation in the yaw plane in the upward and downward phases of a launch before and after autotomy. Figure 8 depicts the yaw undergone by one subject with a full tail during launches in the room temperature and cold conditions. Note the periods of time during which the rate of change of yaw slows on both the way up and down at room temperature, suggesting that the animal can do something to change yaw amount and velocity. Nevertheless, when all data were taken into account, there was no significant difference in the amount of yaw observed between animals with and without tails (Full tail: $M = 69.9$ degrees, $SD = 12.5$ degrees versus Autotomized tail: $M = 73.4$ degrees, $SD = 14.2$ degrees); $t(3) = -1.67$, $p = 0.19$. Additionally, there was no significant difference in the amount of yaw in the down phase between conditions (Full tail: $M = 69.9$ degrees, $SD = 13.3$ degrees versus Autotomized tail: $M = 63.8$ degrees, $SD = 11.6$ degrees); $t(3) = 1.08$, $p = 0.36$ (Figure 9).

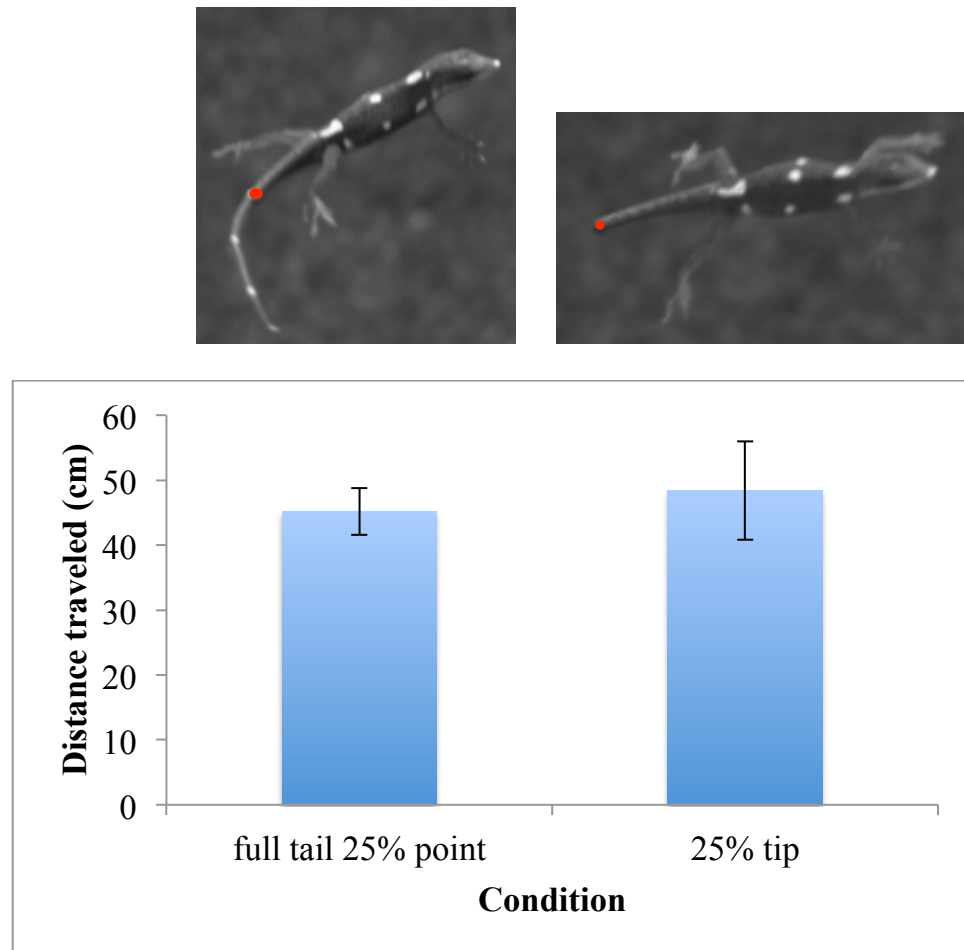


Figure 7. Mean distance traveled by homologous tail points before and after autotomy in room temperature condition. The photos above the conditions represent the points that were digitized to collect data for this analysis. These data are from four subjects and four trials per subject for a total of 16 values per condition. There is no significant difference between conditions ($p = 0.16$).

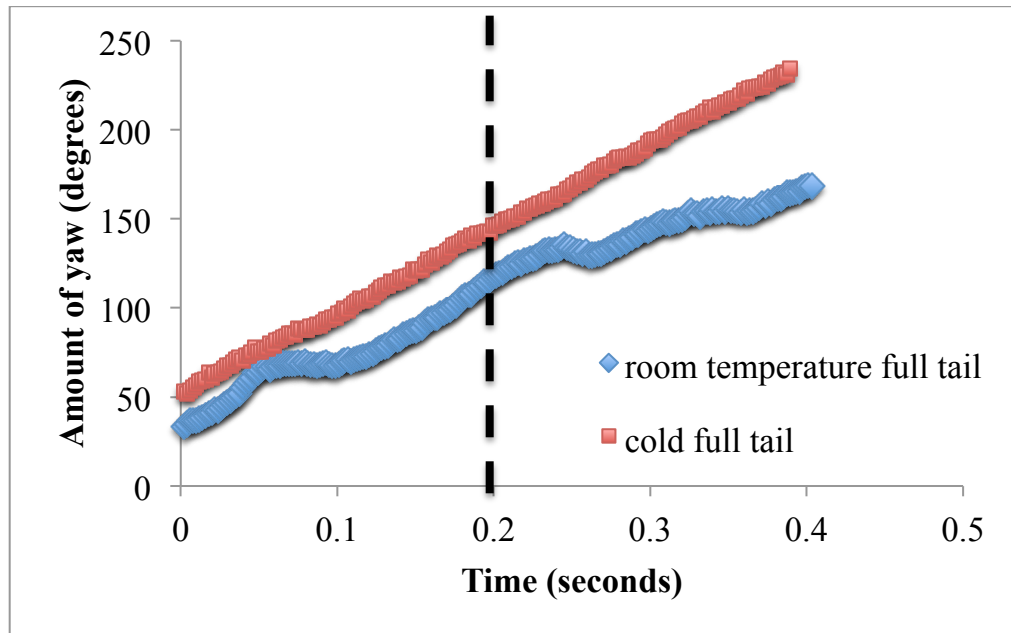


Figure 8. Total rotation in the yaw plane of one subject with a full tail during launches in room temperature and cold conditions. At room temperature, during the up phase, the subject rotates ~83 degrees. During the down phase, the subject rotates ~53 degrees. In the cold condition, during the up phase, the subject rotates ~89 degrees. During the down phase, the subject rotates ~92 degrees. The apex of the launch occurs at about 0.2 seconds for both conditions (dashed line).

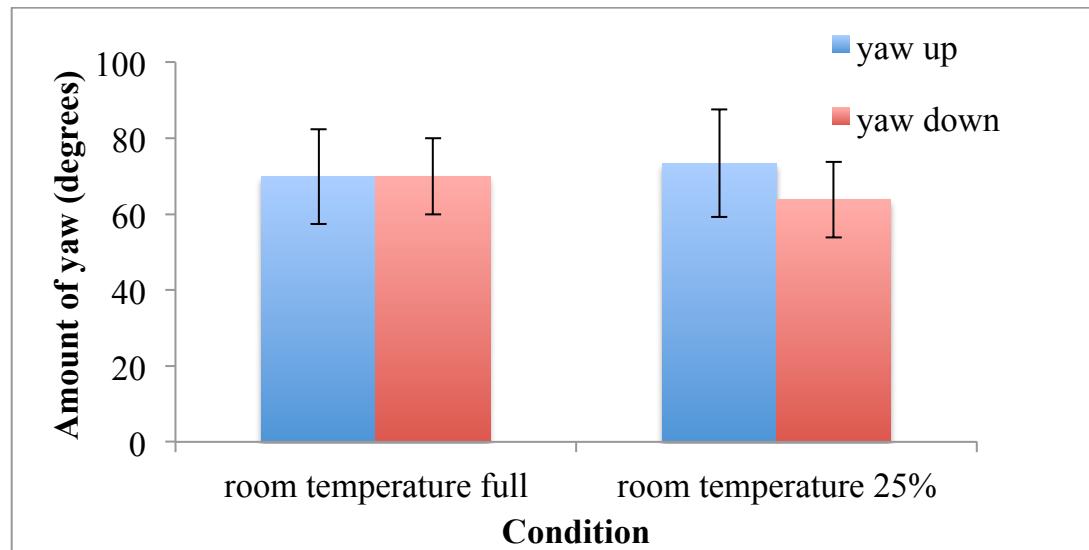
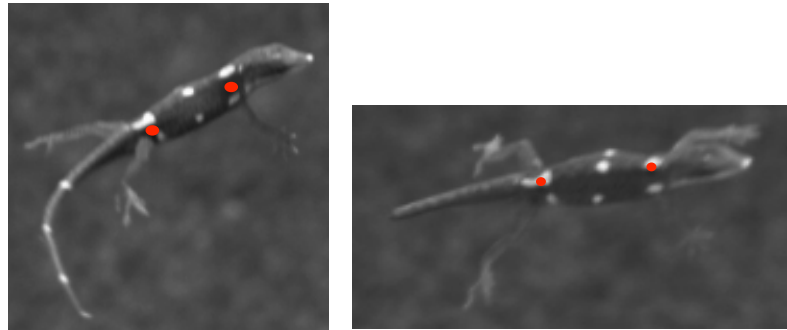


Figure 9. Mean amounts of yaw during up and down phases of the launch at room temperature before and after autotomy. The photos above the conditions represent the points that were digitized to collect data for this analysis. These data are from four subjects and four trials per subject for a total of 16 values per condition. There is no significant difference between conditions (yaw up: $p = 0.19$; yaw down: $p = 0.36$).

The landing angle of the body at the end of each launch was compared in the room temperature full tail and room temperature 25% tail conditions. There was a significant difference in the landing angle in the room temperature full tail condition ($M = 9.12$, $SD = 3.67$) and landing angle in the room temperature 25% tail condition ($M = 4.87$, $SD = 2.86$); $t(3) = 7.36$, $p = 0.005$ (Figure 10). There was no significant difference in the landing angle in the room temperature full tail condition ($M = 9.12$, $SD = 3.67$) and landing angle in the cold full tail condition ($M = 4.85$, $SD = 0.907$); $t(3) = 2.10$, $p = 0.13$.

The angle of the head after destabilization by the launch was calculated with respect to the body of the subject. Figure 11 depicts the angle of the head of one subject with its full tail during a launch at room temperature. Note the starting, minimum, and final head angles. The animal starts with a certain head angle, generally 10-20 degrees inclined relative to the body axis. That angle decreases after destabilization over the first half of the launch and is then brought back to an angle close to where it started. The head angle excursions were compared in the room temperature full tail and cold full tail conditions. There was no significant difference in the initial change in head angle between conditions (Warm: $M = 15.5$ degrees, $SD = 8.61$ degrees versus Cold: $M = 12.2$ degrees, $SD = 5.12$ degrees); $t(3) = 0.563$, $p = 0.61$. However, there was a significant difference in the second head angle excursions between conditions (Warm: $M = 15.9$ degrees, $SD = 5.45$ degrees versus Cold: $M = 4.87$ degrees, $SD = 2.20$ degrees); $t(3) = 3.33$, $p = 0.045$ (Figure 12). The head angle excursions were also compared in the room

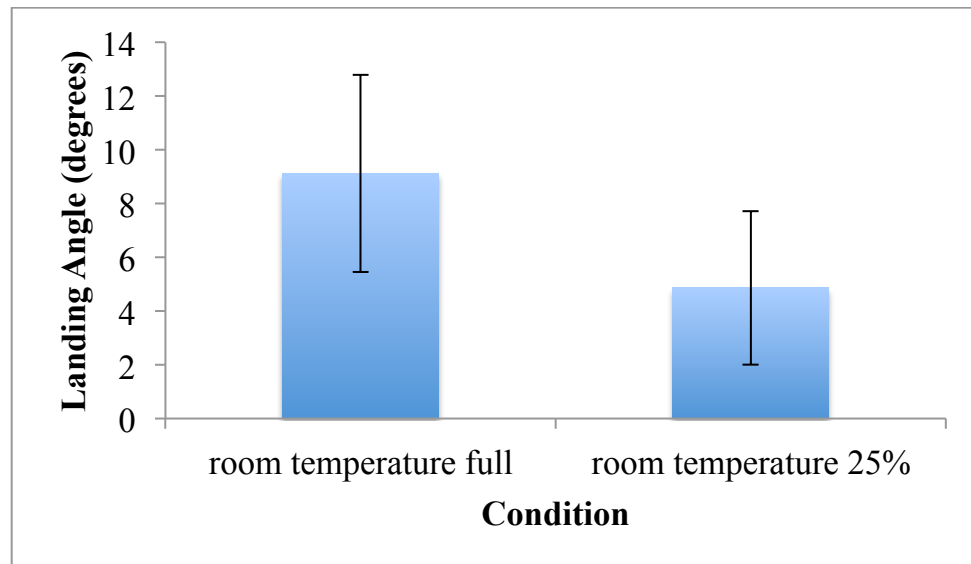
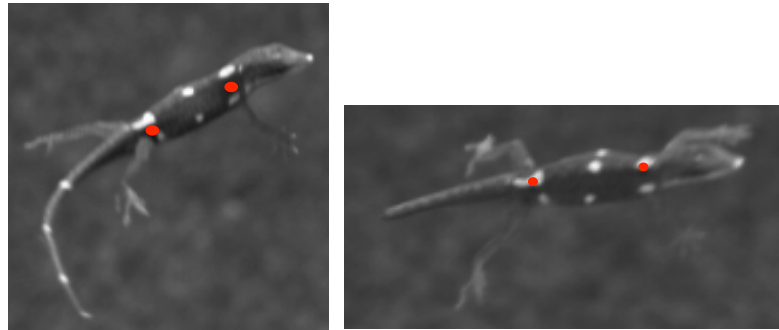


Figure 10. Mean landing angle at room temperature before and after autotomy. This is the landing angle of the body with respect to the platform (i.e., horizontal plane). The photos above the conditions represent the points that were digitized to collect data for this analysis. These data are from four subjects and each subject represents four values per condition for a total of 16 values per condition ($p = 0.005$).

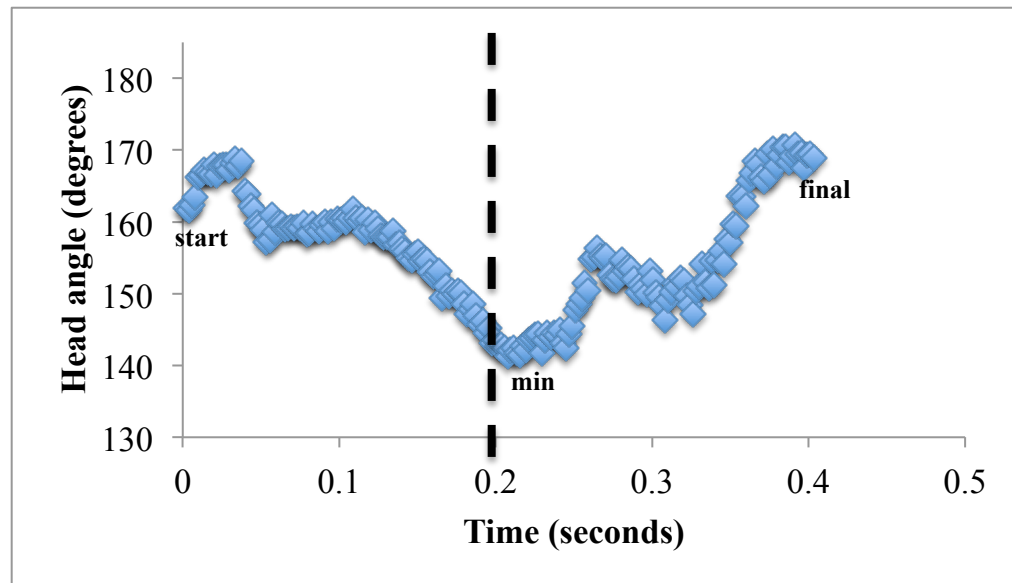
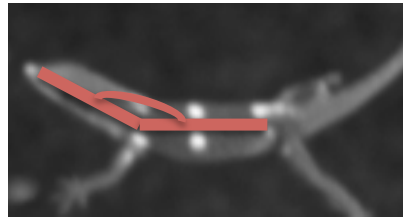


Figure 11. Head angle of one subject with its full tail at room temperature.

The photo above the graph represents how the head angle was measured to collect these data. Movement of the head along vertically and caudally results in a smaller head angle and vice versa. Note the starting head angle (“start”) (~160 degrees), the minimum head angle (“min”) (~140 degrees), and the final head angle (“final”) (~170 degrees). The minimum head angle occurs at about the halfway point or the apex of the launch (dashed line). Most launches exhibit similar patterns in head angle, with an initial change away from the starting angle followed by a subsequent return toward the starting angle.

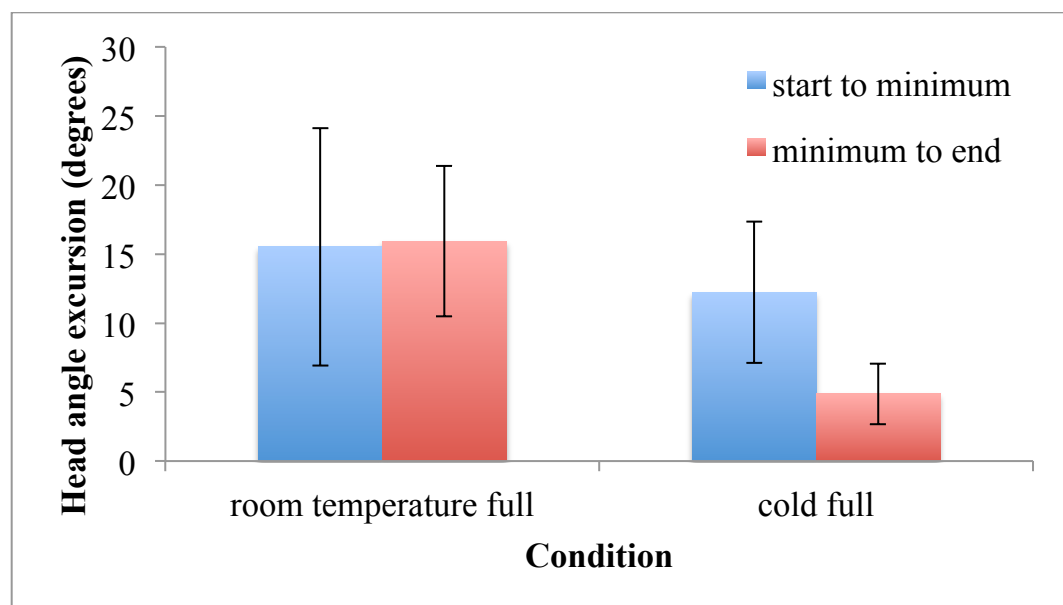


Figure 12. Head angle excursions in room temperature and cold full tail conditions. This is the total change in the head angle from the starting to minimum head angle and from the minimum to final head angle. The photos above the conditions represent the three points that were digitized to collect the angle data for this analysis. These data are from four subjects and each subject represents four values per condition for a total of 16 values per condition. There is no significant difference in the start to minimum head angle excursions between conditions ($p = 0.61$). There is a significant difference in the minimum to end head angle excursions between conditions ($p = 0.045$).

temperature autotomized and cold autotomized conditions. There was no significant difference in the initial change in head angle between conditions (Warm: $M = 12.4$ degrees, $SD = 5.35$ degrees versus Cold: $M = 16.9$ degrees, $SD = 8.64$ degrees); $t(3) = -0.644$, $p = 0.57$. However, there was a significant difference in the second head angle excursions between conditions (Warm: $M = 17.9$ degrees, $SD = 2.67$ degrees versus Cold: $M = 7.88$ degrees, $SD = 3.66$ degrees); $t(3) = 11.3$, $p = 0.0010$.

DISCUSSION

I conducted my study in order to explore three principal questions. First, do green anoles actively engage their tails in response to a destabilization in the yaw plane? Second, do animals change tail movement behavior after 75% caudal autotomy to compensate for tail loss? Third, after autotomy, are tail stump movements, if present, successfully stabilizing the animal or are the animals experiencing decreasingly coordinated outcomes with respect to the yaw destabilization?

Tail use in response to a destabilization

I hypothesized that lizards would engage the tail in side-to-side movements in response to a destabilization in the yaw plane. These qualities were observable in the majority of launches in which animals were at room temperature and able to make voluntary movements (Figure 5). Since green anoles and lizards in general are ectotherms, cooling of the body for the cold trials limited tail movements and served as a control for the room temperature trials. The average distance traveled by the tail at room temperature was greater than the average distance in the cold condition. However, the anoles did not move their tails enough at room temperature compared to the cold condition to suggest that they are actively making those movements to correct for the destabilization in the yaw plane. Due to the variability in pre-autotomy tail length between subjects,

distances traveled by the tip of the tail were also inconsistent between subjects. A follow-up study with more similarly sized subjects could produce significant findings. Nevertheless, the lack of a significant difference between conditions suggests that using the tail to actively control yaw instability may not be an important strategy employed by these animals. Comparisons of distance traveled by the tail before and after caudal autotomy can suggest whether lizards attempt to compensate for partial tail loss by swinging the stump further and faster after the destabilization.

Effects of autotomy on tail use

There is evidence that suggests that lizards may behave differently pre and post autotomy in the wild. A study by Downes & Shine (2001) suggests that tailless lizards (*Lampropholis guichenoti*) have a tendency to flee sooner than tailed individuals in response to the presence of a predator. Martín and Salvador (1997) indicate that tail loss in a different species (*Lacerta monticola*) leads to reduced amounts of conspicuous behaviors, such as movement and mate searching, due to increased risks of predation. A study by Formanowicz et al. (1990) reveals that the ground skink, *Scincella lateralis*, also reduces general activity and the distance traveled after autotomy. Furthermore, activity may be limited to the middle of the day since low, early-morning and evening temperatures combined with compromised locomotor skills increase predation

risk. Finally, lizards might also exploit different habitats after caudal autotomy, as demonstrated by Irschick and Losos (1999).

Fewer studies have investigated how the tail (or what remains of it) is used following autotomy compared to pre-autotomy usage. Given the emphasis of previous studies on the importance of the tail in lizards for controlling pitch and roll of the body in mid-air, I chose to study whether anoles would alter in-air tail movements after caudal autotomy in order to compensate for the loss in tail length. Findings indicate that the tail did not travel significantly farther after autotomy. It's possible that more subtle differences in the ways they moved their tails might occur, as total distance is a somewhat crude measure of the complex movements undertaken by the tail during destabilization events. Nevertheless, these anoles do not appear to change their tail movement behavior post-autotomy to compensate for having less tail in order to correct any instability in the yaw plane.

Effects of caudal autotomy on in-air stability

In this study, the destabilization was limited largely to the yaw plane to investigate the tail's response. To test whether loss of the tail leads to increased instability, I measured the total amount each subject rotated in the yaw plane during the up and down phases of a launch. Animals yawed slightly more, on average, during the up phase, but then slightly less during the down phase after autotomy. However, these differences were not significant, which suggests that losing the tail has no effect on yaw destabilizations, likely because animals are not

using their tail to correct for such destabilizations. Such a lack of a correction for yaw also suggests that destabilizations in this plane are less important to the animal, perhaps because they pose less of a threat to coordinated landing. Yaw allows the animal to remain roughly parallel to the ground, unlike pitch and roll, which if not corrected, could result in disastrous landings on the head or back.

In addition to assessing yaw, I also examined the body angle at which anoles landed after the launch and found that anoles without their tails landed with a slightly smaller angle (more parallel to the ground) than those with their tails. This is unexpected, however, the actual differences in landing angle, namely, 9 degrees in animals with tails versus 5 degrees in animals without, is likely functionally not important. Furthermore, observations of the videos revealed that animals always landed hind end first, never head first. Therefore, in neither condition was the head ever in danger of making the first ground collision upon landing. Additional examination of head angles throughout flight could provide insight as to whether or not the tail might contribute to head stability control.

One proposed reason for tail movements during in-air destabilization, besides that of body stability, could be to control head movements in order to stabilize the visual system. This would allow the animal to keep a steady gaze on where it is moving and/or what surrounds it. Due to the motor control center's location in the head, it is likely important to maintain constant head angles for body control and coordinated landing. Therefore, I returned to comparisons

between the room temperature and cold conditions for full tailed animals and for tailless animals, and I measured how much the head angle changed after the initial launch. This change amounted to 10-15 degrees and was not significantly different across conditions. These results are likely due to the consistency in destabilization for each launch no matter the condition. Following this initial change in head angle, most animals also showed a return in the head's orientation toward its original angle at launch. This "corrective" head movement differed significantly between the room temperature and cold conditions for tailed animals. This could potentially imply that the active tail movements available to warm animals contributed to head angle corrections. However, as stated previously, subjects did not move their tails significantly more at room temperature than when cold. There also does not appear to be an effect of the tail since the difference between conditions was also significant for tailless animals. Therefore, it seems more likely that head angle corrections are due to an individual's ability to simply move its head up and down when unimpaired by temperature, and head angles do not relate to tail movements at all.

Tail as a control for complex destabilizations

The tail plays an important role in correcting for rotation of the body in the pitching axis (Gillis et al., 2009) and in the rolling axis (Jusufi et al., 2008; Jusufi et al., 2011). As demonstrated in this study, the tail does not appear to play such an active role in correcting for yaw rotation of a lizard's body. In a typical jump

or fall, an animal can experience instabilities in any or all of these axes of rotation. Since the animal is likely more at risk of injury as a consequence of substantial pitching or rolling, since both of these destabilizations can lead to a landing on parts of the body other than the limbs, it is reasonable to hypothesize that the animal does not attempt to correct for yaw. Or, perhaps the anoles did not experience enough instability to necessitate tail activity to correct for it. The lack of a difference in the amount of yaw rotation pre and post autotomy supports the notion that tail movements are not controlling yaw alterations.

CONCLUSIONS

Severe rolling of the body in mid-air could cause an animal to land on its back or side and extensive pitching of the body could cause an animal to land on its head. Extreme yawing only results in a change in the direction the animal is facing after landing. As long as the animal reacts to and corrects for pitch and roll, the amount of yaw should not be detrimental to coordinating a successful landing. Tail movements themselves do not appear to control for yaw instability. Furthermore, caudal autotomy does not appear to elicit a behavioral change in how the tail is used in response to a yaw destabilization. Finally, tail loss does not affect how much the animal rotates in the yaw plane so it must not use the tail to make this type of correction. Any disruption of the head's position is probably corrected for by movement stemming from the neck rather than as a result of tail motion. In conclusion, landing coordination after destabilization in the yaw plane alone is not controlled for in these anoles.

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