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JUMPING BEHAVIOR AND THE EFFECTS OF CAUDAL AUTOTOMY ON
PERFORMANCE IN *ANOLIS CAROLINENSIS*

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

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May, 2007

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

To my parents and sister
for being my support system
from the beginning...

ACKNOWLEDGMENTS

I thank Professor Gary Gillis for sparking my interest in research and being a wonderful advisor. I owe much of my success (and sanity) at Mount Holyoke to you.

I also thank University of Massachusetts Professor Duncan Irschick for being a member of my thesis committee and providing help in the planning and execution of my morphology and behavior experiments.

Professor Stan Rachootin for being a member of my thesis committee and comic relief during my six-week all-nighter.

Emily Goldstein, Dery Miller, Noelle Noyes, Alli Haley, and Lindsay Goodale for their moral support and help in experiments and animal care.

Professor George Cobb for his assistance in the statistical analysis of my data.

Debbie Piotrowski and animal care staff for assisting with animal care.

The Mount Holyoke College Biology Department for providing me with an amazing education and the funding that fueled my research.

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ABSTRACT

Maximal locomotor performance in Anolis lizards has been studied extensively within and across species. Hindlimb length is correlated with jump distances in a number of species of anoles, and differences in the structural habitat can have effects on individual performance. *Anolis carolinensis* lizards were videotaped undisturbed in two habitat matrices of different perch densities. Neither maximal performance nor morphological features appear to affect locomotor behavior.

Caudal autotomy, or tail-loss, is an anti-predator strategy in a variety of lizard species, including anoles, and presents immediate benefits to the animal, allowing for survival in an otherwise potentially fatal situation. However it is also accompanied by numerous costs including changes in locomotor ability. For example, sprint speed, climbing speed, and endurance are affected in different species of lizards. *A. carolinensis* use jumping frequently as a form of locomotion, often have long tails, and have the ability to autotomize their tails as an anti-predator strategy. Before autotomy, the angle of a lizard's body during jumping remains slightly above the horizontal throughout the jump. Following autotomy, body angles are extremely variable, and jump distances may be reduced.

INTRODUCTION TO *ANOLIS CAROLINENSIS*

Anolis lizards, commonly called anoles, are a genus of approximately 300-400 species of relatively small, insectivorous lizards, of which approximately half live on Caribbean islands and surrounding mainland (Losos 1994). Each island in the Caribbean has its own unique set of anoles, ranging in diversity from 1-2 species on small islands to approximately 40 species on the larger islands of Hispaniola and Cuba (Losos 1994). The anole species on each island evolved to partition their resources along three axes: prey size, microclimate or thermal habitat, and structural habitat (Losos 1994). Species partition structural habitat by perch height and diameter (Irschick and Losos 1999). The partitioning is most likely due to competition, since resources appear to be limiting and neither predation nor differential parasitism seem to affect anole community structure or habitat use (Losos 1994).

Each species of anole belongs to one of six ecomorphs, named based on their structural habitat use. Anoles can be categorized as crown giants, trunk-crown, trunk, twig, trunk-ground, or grass-bush ecomorphs (Losos 1994, Toro et al. 2004). Ecomorphs are groups of species that are not necessarily closely related, but occupy the same habitat or niche, and can generally be characterized

by similar morphology (Losos 1994, Toro et al. 2004). For example, lizards categorized into the twig ecomorph are specialized for living on twigs. Their limbs are short to facilitate balancing while moving on thin branches (Losos and Irschick 1996). Reliable phylogenetic trees for anole evolution only exist for Jamaican and Puerto Rican anole species (Losos 1994). Both islands show a similar macroevolutionary pattern of sequential ecomorph evolution (Losos 1994). Though there are not enough data to draw any significant conclusions, it seems as though species first diverge to partition their structural habitat, followed by specialization in microclimate or prey size (Losos 1994).

All anoles are specialized for arboreal locomotion, and are equipped with toe pads for dry adhesion to their substrate. Their toe pads are covered by many transverse scales called lamellae. Each lamella is covered in numerous setae, or tiny keratinous “hairs”, which are each covered with many smaller projections. These smallest projections ultimately interact with the substrate via Van der Waals forces, which allow the lizards to adhere to almost any surface (Macrini et al. 2003). This method of adhesion allows the lizards to climb, sprint, and jump effectively through their habitats.

Since anoles are so adept at arboreal locomotion, many studies of locomotor performance have focused on their jumping, climbing, and sprinting capabilities. The species I chose to use in my studies is *Anolis carolinensis*, commonly known as the Green Anole. The species is native to the southeastern United States, and are the most northerly distributed species of anole. They live as

south as subtropical Florida, north to temperate Oklahoma and Tennessee (Jenssen et al. 1998). Lizards of this species have the ability to change color from dark brown to vibrant green, depending on their body temperature, mood, or surroundings. Their dewlaps range in color from white to red, and are used in sexual, advertising, and aggressive displays. Adults range in total length from approximately 12-20 cm. Males are larger than females, and have larger, brighter dewlaps, enlarged dorsal crests, and enlarged postanal scales. Male size is positively correlated with social dominance, territory size, and harem size (Andrews 1985).

The species belongs to the trunk-crown ecomorph. Members of the trunk-crown ecomorph are fairly generalized and can be found in a variety of arboreal and human-made habitats. In natural settings, the anoles live in palmetto scrub, seagrape bush scrub, cypress-tupelo swamp, and deciduous hardwood forests (Jenssen et al. 1998). In urban areas, the lizards live in plantings and along fences and walls (Jenssen et al. 1998). The highest densities of individuals are in areas with breaks in the canopy, usually from water bodies, trails, and fields (Jenssen et al. 1998).

I chose to perform my studies on *A. carolinensis* because there have been numerous studies of their locomotor performance and behavior in the laboratory and in the field. They are easily accessible, can be kept in captivity, and are manageable for conducting experiments. In this thesis I explore the relationship between jumping behavior and morphology in anoles in two separate studies. First

I examine whether links exist between body and limb morphology and locomotor activities in a controllable structural habitat. In particular, I address whether traits associated with high levels of maximal performance (e.g. limb length (Toro et al. 2003)) are also tightly coupled with submaximal activities. For example, do longer limbed lizards jump more frequently, or over greater distances, on average, than short-limbed con-specifics? Second, I quantify the effects of tail autotomy on jumping performance. Specifically, I determine if tail loss leads to decreased jump distances or lowered control of body movement during jumping. Both studies are aimed to fill current gaps in our knowledge of lizard jumping behavior.

CHAPTER 1

MORPHOLOGY AND BEHAVIOR IN GREEN ANOLES

INTRODUCTION

Maximal locomotor performance in *Anolis* lizards is well studied within and across species (Irschick and Losos 1999, Losos and Irschick 1996, Toro et al. 2003, Toro et al. 2004, Toro et al. 2006). Maximal sprint speeds and jump distances in anoles can be correlated with size differences (Toro et al. 2003, Toro et al. 2004, Toro et al. 2006), hindlimb kinematics and force output (Toro et al. 2004, Toro et al. 2006), and environmental characteristics (Irschick and Losos 1999, Losos and Irschick 1996). Despite the many studies exploring maximal locomotor capacities in these lizards, very little is known about their more natural, submaximal activities. As a result, in this study, I chose to focus on the relationship between morphology and jumping behavior during undisturbed conditions to see if traits associated with maximal performances are also tied to more typical locomotor activities.

Bels et al. (1992) characterized *Anolis carolinensis* jumps into four distinct phases: initiation or hindlimb posturing, takeoff, flight, and landing (Figure 1.1). During the initiation phase, the lizard swings its hind limbs up and forward, such that its hind feet are in front of its center of balance, close to its forelimbs. The forelimbs are lifted off the substrate and the hindlimbs are

extended during the takeoff phase, which lasts until the lizard is no longer in contact with the substrate. The flight phase is the entire length of time that the lizard is not in contact with the substrate. The landing phase is initiated when the lizard comes back into contact with the substrate. The most important of these four phases for the studies of maximal performance is the takeoff phase, when force is being generated to accelerate the animal.

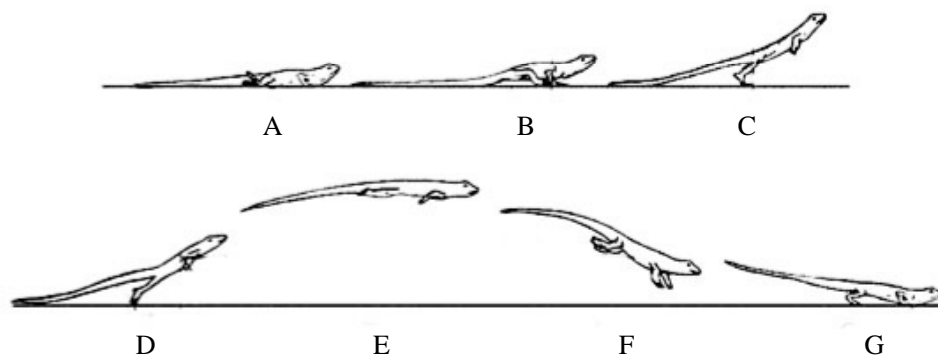


Figure 1.1. Stages of *Anolis* jumping: hindlimb positioning (A & B), takeoff (C & D), flight (E & F), and landing (G) (Adapted from Toro et al. 2004).

Hindlimb morphology clearly correlates with locomotor performance in *Anolis* lizards. Jump distance increases with limb length in *Anolis sagrei*, *Anolis equestris* and *A. carolinensis* (Toro et al. 2003). The positive correlation between hindlimb length and jump distance makes sense because limb length is an important factor in determining the length of time the lizard is able to exert a force on its substrate during the takeoff phase of a jump. Longer limbs mean extended durations for generating force against the substrate. By increasing the time that force is exerted, the lizard has more time to accelerate its body up and

forward and thus can attain a higher velocity at takeoff (Biewener 2003). If the angle of takeoff is equal, a lizard leaving the ground with a high velocity at takeoff will travel farther horizontally than a lizard with a lower velocity.

There is no correlation between morphology and takeoff angle (Toro et al. 2003, Toro et al. 2004), and escape jumps of *A. carolinensis* have an average takeoff angle of approximately 30 degrees above the horizontal (Bels et al. 1992). In ballistics, the initial velocity at takeoff and the angle of takeoff determine the horizontal distance traveled by a projectile object. The optimal angle of takeoff for a simple projectile is 45 degrees to the horizontal. However, in jumping animals, takeoff angles ranging between approximately 30-55 degrees lead to little difference in the overall distance jumped (Marsh 1994). By reducing takeoff angle to only 30 degrees, the lizards reduce their jump distance minimally, but they are able to shorten their flight duration and height significantly (Bels et al. 1992). Reduction in takeoff angle, flight duration and height allows the lizard to use less energy per unit distance, avoid hitting nearby branches during flight, and reduce the amount of time it is in the air and vulnerable to predators (Bels et al. 1992). The selection for a relatively low takeoff angle is similar across individuals of varying morphological dimensions, suggesting the global importance of energy conservation as well as reduced flight duration and height among jumping lizards.

It is common for studies of lizard locomotion to reveal substantial intraspecific variation in performance (Garland and Losos 1994). During jumping, since takeoff angle tends to be constant across individuals, another mechanism

underlying such variation must exist. In many species, the lengths of distal segments of a limb are correlated with locomotor performance. Higher takeoff velocities would result from the reduction of rotational inertia on the limbs as distal segments increase in length (Toro et al. 2004). However, in *Anolis* species it seems that only total limb length is correlated with takeoff velocity and jump distance, which may be because jumps consist of a single motion, so rotational inertia would not impact locomotion as negatively as in a cyclical gait (Toro et al. 2004). Variation in jumping capacity could also be caused by differences in limb muscle size, or physiological differences in muscle composition (Toro et al. 2004). Variation in muscle composition is highly unlikely, and instead, differences in muscle size likely contribute the most to variation in jump distance among lizards with similar hindlimb lengths (Toro et al. 2004).

An animal's structural environment can also affect its locomotor performance. For example, in animals that use tree branches as their perches, sprint speeds decrease as perch diameters decrease, especially in long-limbed individuals (Irschick and Losos 1999, Losos and Irschick 1996). This may be a result of the animals' reduced gripping ability and difficulty keeping their center of balance over a narrow support (Irschick and Losos 1999). Unlike sprint speeds, jumping abilities in anoles appear to be unaffected by perch diameter (Losos and Irschick 1996). Although anoles commonly use maximal sprint speeds to escape predators, escape behaviors are affected by the animal's structural habitat (Losos and Irschick 1996). Since jump distance is not obviously affected by small perch

diameters, individuals tend to use jumping more often to escape disturbances in habitats with narrow perches (Losos and Irschick 1996). Jumping frequency also increases in cluttered habitats, so lizards tend to jump more as perch density increases (Irschick et al. 2000, Moermond 1979, Pounds 1988).

Performance and escape behavior not only vary across individuals of the same species, but also within an individual during ontogeny. Hindlimb length grows with negative allometry in *A. carolinensis* (i.e. larger animals have relatively smaller limbs) and in direct proportion to body size in most other species of anoles (Toro et al. 2003). Juvenile *Anolis lineatopus* and *Anolis gundlachi* tend to jump more frequently than adults, and make short jumps between adjacent perches (Irschick et al. 2000). Jenssen et al. (1998) noted that juveniles are better than adults at navigating on narrow and flexible perches, such as leaves and grasses. Juveniles also tend to stay in lower, more cluttered environments (Jenssen et al. 1998) and employ different escape strategies than adults (Irschick et al. 2000). Juveniles may find crypsis and navigation of escape routes easier in lower, more cluttered environments (Jenssen et al. 1998), while adults use higher and wider perches (Irschick et al. 2000, Jenssen et al. 1998). Over time, growing individuals alter their behavior and move from lower habitats to the higher habitats used more frequently by adults.

Increased locomotor performance facilitates predator evasion and prey capture, but the role of performance in other ecologically important behaviors is not as well studied. Social dominance in *Anolis* lizards is correlated with sprint

speeds (Garland Jr. et al. 1990), which shows that performance may have an effect on behaviors other than predator-prey interactions. If morphology and habitat structure have an effect on performance, they may also be correlated with actual behaviors and habitat use. For example, individuals may maximize their fitness by choosing habitats that complement their maximal capabilities best (Irschick and Losos 1999, Losos and Irschick 1996). However, Garland Jr. et al. (1990) found that there was no correlation between maximal capacity and behavior, which they claim reflects the fact that ectotherms use submaximal activity often enough that performance does not limit most behaviors.

Given the potential importance of submaximal activities in lizards, and the emphasis to date on maximal capacities, I chose to study *A. carolinensis* locomotor behavior during undisturbed conditions and characterized jump distances and frequencies as well as the proportion of time spent walking or running in an artificial perch-rich habitat. My goal was to determine whether differences in morphological variables important to maximal performance, such as limb length, are also linked to variation in submaximal jumping behavior. In addition, by studying locomotor activities in two habitat matrices of different perch densities, I could explore potential relationships between structural habitat and locomotor behavior. I hypothesized that lizards with morphological features such as long limbs, that would improve their maximal performance, would jump farther and move more frequently than lizards lacking such attributes. I also expected more activity in the environment with more densely packed perches,

which would be consistent with previous studies on perch density and habitat use (Irschick et al. 2000, Moermond 1979, Pounds 1988).

MATERIALS AND METHODS

Animals

All wild-caught *A. carolinensis* individuals were purchased from Dave's Soda and Pet City in Hadley, MA and housed in the laboratory at the University of Massachusetts in Amherst, MA. I chose healthy individuals that had completely or mostly original tails. Each individual was maintained in its own 14.5" x 8.5" x 10" plastic tank with plastic leaves and a wooden perch. The room temperature remained around 77°F, so no extra heating lamps were necessary. Tanks were moistened daily Monday through Friday to maintain high humidity, and each lizard was fed four or more small crickets twice per week.

Morphology

The body mass of each lizard was measured to the nearest 0.1 grams. The snout-vent length (SVL), tail length (TL), hindlimb segment lengths (femur, tibia, metatarsals, longest toe), and forelimb segment lengths (humerus, radius, metacarpals, longest finger) of each lizard were measured to the nearest 0.1 mm using fine calipers. To calculate total length, SVL and TL were added together. Total limb lengths were calculated by adding all respective limb segment lengths.

Maximum Jump Performance

The maximum jump distance was measured for each lizard in a small jumping arena consisting of a 10.5 cm-tall cardboard platform covered in fine sandpaper for take-off, and a landing area covered in white paper marked with 2 cm squares to measure the horizontal distance traveled during each jump. Lizards were induced to jump three times each, with a period of approximately 5 minutes rest between trials. All jump distances were recorded, but only the longest distance from each individual was used for data analysis.

Artificial Perch Habitat

The artificial perch habitat was made with a 16.5" x 35" x 48" mesh enclosure purchased from Big Apple Herp (www.bigappleherp.com). To construct perch matrices within the enclosure, 2.5 cm-wide strips of Styrofoam were cut and punched with 1 cm diameter holes at 5 cm intervals. The Styrofoam strips were tied to opposite sides of the enclosure with thread in 3 vertical tiers, 10 cm apart along the longest sides. Dowels, 1 cm in diameter, were cut to 40 cm in length, marked at 5 cm intervals and inserted into the holes in the Styrofoam strips, spanning the width of the enclosure. To prevent the dowels from slipping out of the holes in the Styrofoam strips, their ends were wrapped in duct tape.

Two different perch matrices were designed: setup A with perches 10 cm apart in three vertically offset tiers, and setup B with perches 5 cm apart in two

vertically offset tiers (Figure 1.2). Three 30-inch long rods were distributed through the habitat to allow easy access to perches from the ground. The exposed mesh on the sides of the tank was covered with wax paper and lightly coated with vegetable oil to prevent lizards from leaving the camera's field of view by crawling across the enclosure's sides. During experiments, two heating lamps were hung over the enclosure from a pole suspended between two tripods. A Sony Handycam digital video camera recorder was attached to a third tripod, facing down on the enclosure, keeping as many dowels in view as possible.

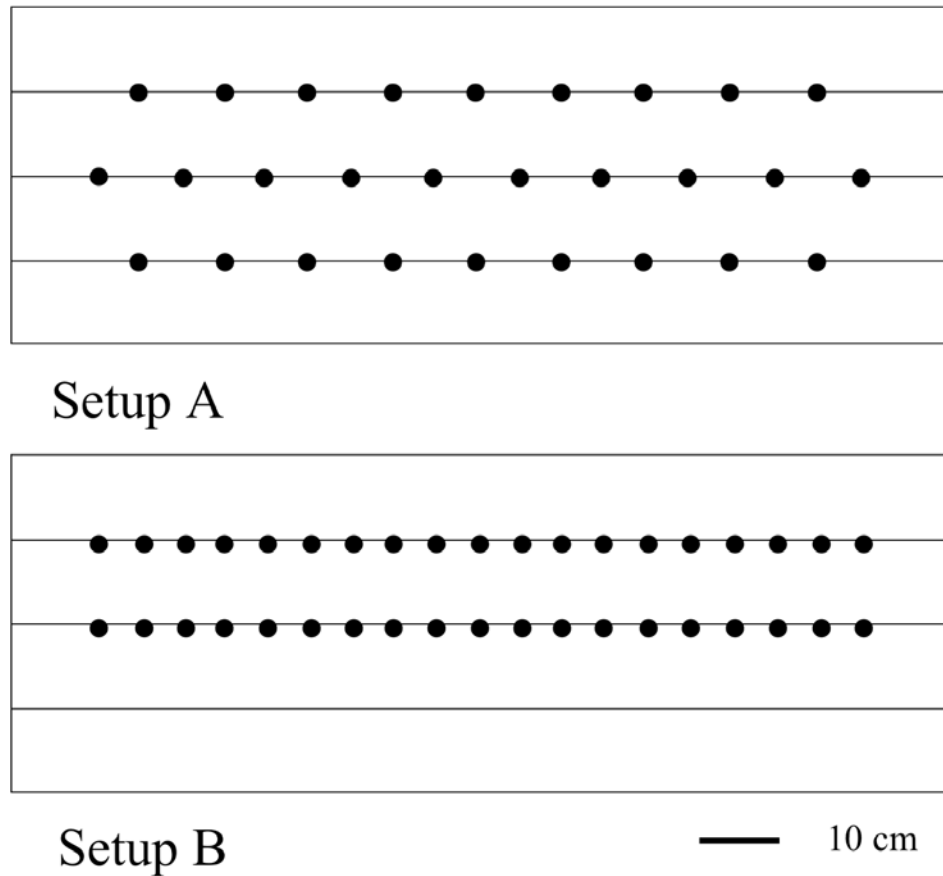


Figure 1.2. Schematic diagrams of cross-sections of the experimental enclosure. Each black dot is the cross section of a 1 cm diameter dowel. In setup A, dowels were placed 10 cm apart in each tier, and the middle tier was offset by 5 cm. In setup B, each dowel was placed 5 cm apart and both tiers were in line. In both setups, tiers were 10 cm apart.

Experimental Procedure

For each experimental trial, a single lizard was placed in the enclosure and its activities were recorded for a total of 3 hours per matrix setup. Individuals had at least 15 minutes to acclimate to the enclosure before video recording began. Each recording session lasted 90 minutes without interruptions. If the second

recording session for an individual in the same perch matrix was scheduled for the next day, the lizard was left in the experimental enclosure overnight.

Some lizards were introduced to setup A first, and some to setup B first. All three hours of video collection were always completed for the first setup before introducing the lizard to its second setup.

Behavioral Data Collection

To analyze videos for locomotor activity and behavior, the number and distance of jumps were recorded while the lizards were in view. In addition, the amount of time that each lizard spent walking or running across dowels or the enclosure walls was also recorded, as was the fraction of time each lizard spent in and out of view of the camera.

The frequency of jumps for each individual in each setup was calculated by dividing the number of jumps made by the number of minutes the individual was in view. I also calculated the proportion of time that each lizard spent walking or running in each setup by dividing the amount of time moving by the amount of time the lizard was in view.

Data Analysis

To explore potential relationships between morphology and locomotor activities, data on movement patterns and jump frequency were plotted against SVL, hindlimb length, and maximum jump distance for each setup. Microsoft

Excel was used to calculate the lines of best fit and corresponding R-square values for each data set. A paired two-sample t-test was performed on the percent time moving between setups A and B using Microsoft Excel to determine if individual behavior varied significantly depending on perch density. The same test was employed to determine the effect, if any, of perch density on jumping behavior.

RESULTS

Maximal jump distances of the lizards ranged from 20 cm to 34 cm and averaged 28.2 cm. Maximum jump distance was unrelated to hindlimb length ($R^2 = 0.06$) or any other morphological variables measured in this study (Figure 1.3).

Lizards in the artificial enclosures spent 1.3% of their time, on average, actually moving. This varied substantially among individuals and ranged from 7.3% in the most active animal to 0.02% in the least active animal. Jump frequencies also varied dramatically among individuals and ranged from 0.03 to 0.46 jumps/minute (mean = 0.17 jumps/minute).

Average jump distances in each setup were difficult to compute, since some lizards made jumps of unknown distances to or from the walls of the enclosure and ground access perches (nine of the 104 jumps made in setup A and two jumps in setup B were of unknown distances). Without taking into account the jumps of unknown distances, the average jump distance was 10 cm in setup A and 5.36 cm in setup B. In general, lizards jumped only to adjacent dowels on the same tier, and made consecutive jumps to travel distances farther than the inter-perch distances. Only one individual jumped from the top tier to a perch in the lower tier in setup B, for a jump distance of 25 cm. The majority of jumps were made only along the top tier in both setups. With the exception of the jump from

the top tier to the second tier, all lizards accessed the second tier by walking or jumping onto perches from one of the long access poles or the enclosure wall.

The mean percent time moving for setup A was 1.94%, and the mean for setup B was 0.69%. However, these values were not statistically significantly different from one another ($P = 0.12$ in a one-tailed paired t-test. The mean number of jumps per minute was 0.13 in setup A and 0.21 in setup B, values that also were not significantly different from one another ($P = 0.14$).

Jump frequency showed no relationship with SVL, hindlimb length, or maximum jump distance in either setup (Figure 1.4). The amount of time each lizard spent walking or running in the enclosure also did not appear to be related to SVL, hindlimb length, or maximum jump distance in either setup (Figure 1.5). The lines of best fit for each plot did not show any significant correlations between any variables (Table 1.1).

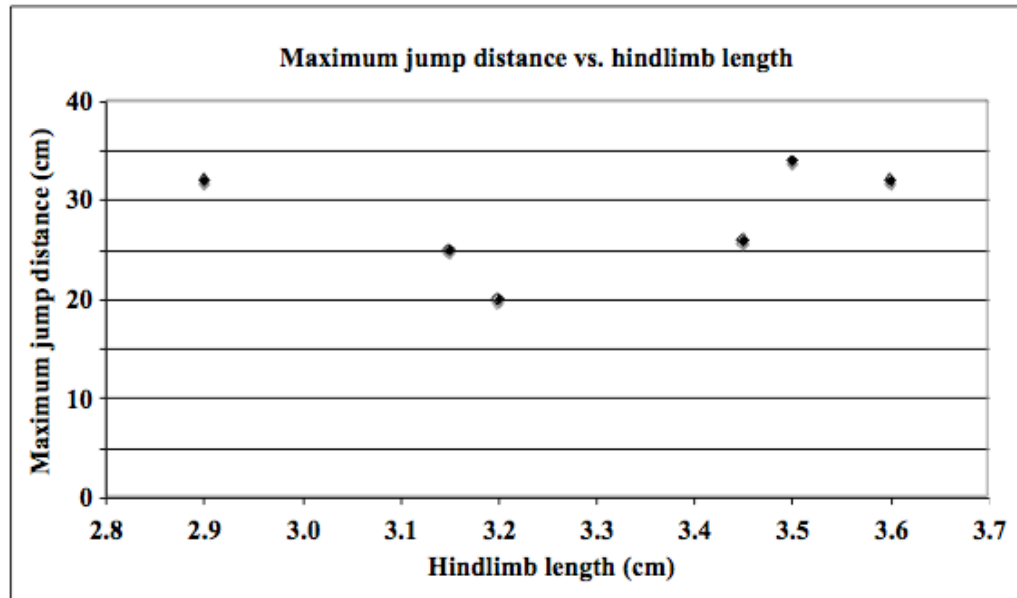


Figure 1.3. Maximum jump distances plotted against hindlimb length. Note that there is no clear relationship between jump performance and hindlimb length.

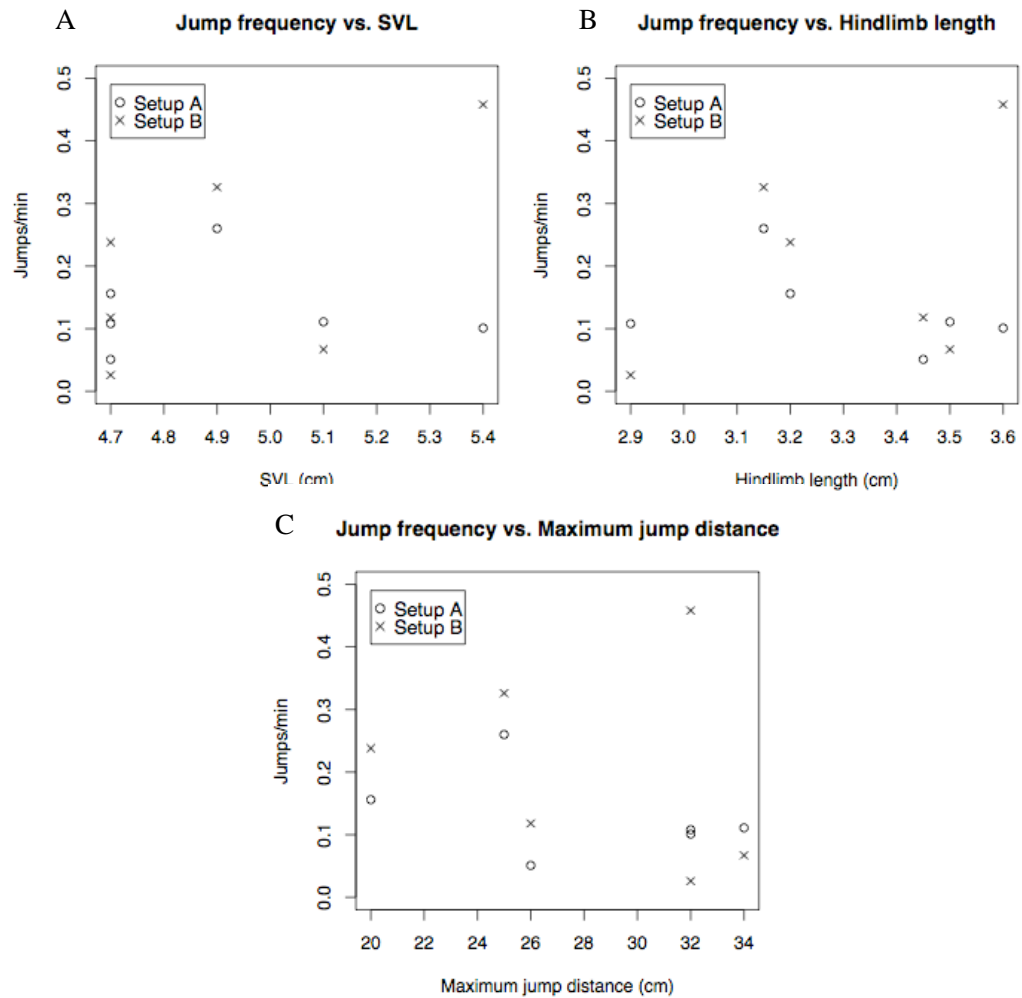


Figure 1.4. Jump frequency plotted against (A) snout-vent length, (B) hindlimb length, and (C) maximum jump distance.

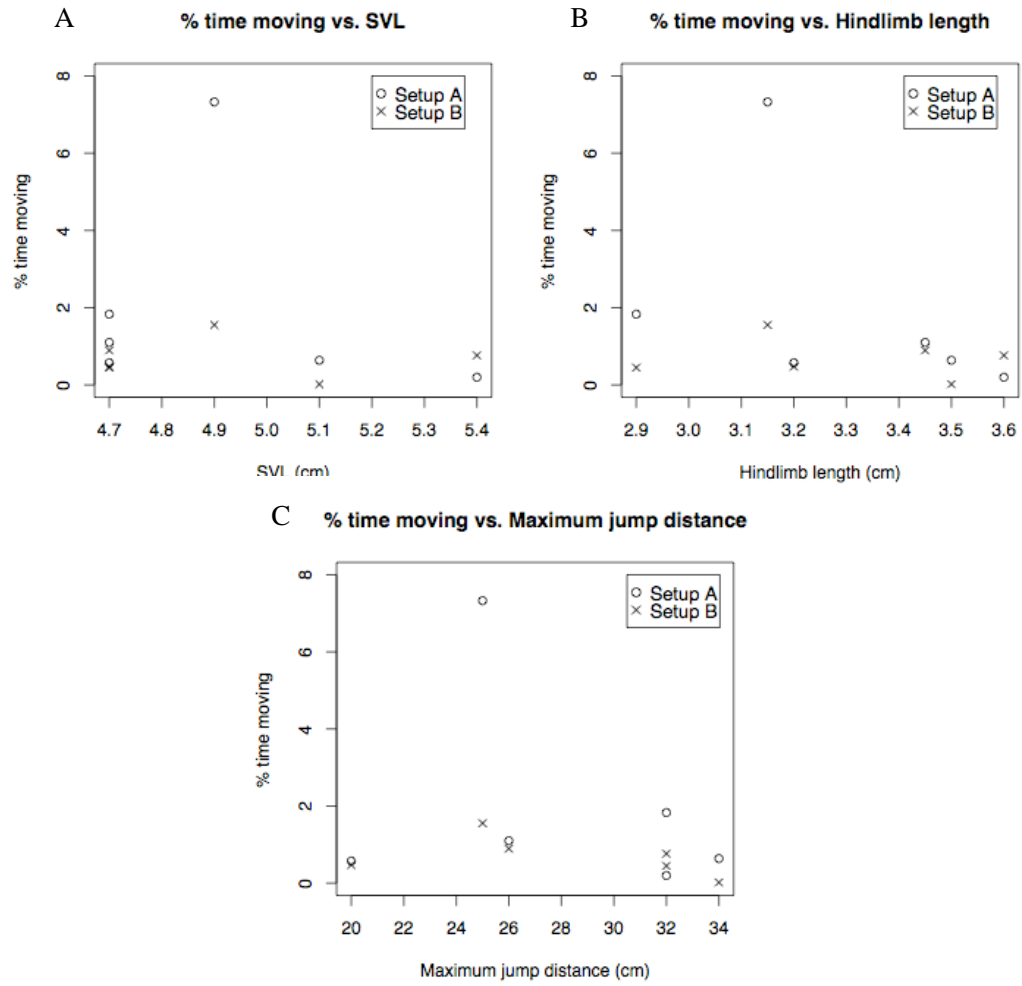


Figure 1.5. Percent of time spent moving plotted against (A) snout-vent length, (B) hindlimb length, and (C) maximum jump distance.

Table 1.1. The slopes, intercepts, and R square values for the lines of best fit in each setup for each relationship.

Relationship	Setup	Slope	Intercept	R Square
% time moving vs. SVL	A	-1.6359	9.9865	0.0302
	B	-0.1145	1.2553	0.004
% time moving vs. HL length	A	-4.4491	16.6255	0.1885
	B	-0.2686	1.5784	0.0184
% time moving vs. max jump	A	-0.1294	5.5874	0.0669
	B	-0.0413	1.8543	0.1827
Jump frequency vs. SVL	A	-0.0083	0.172	0.0011
	B	0.3562	-1.5456	0.3737
Jump frequency vs. HL length	A	-0.1092	0.4914	0.1623
	B	0.2475	-0.6111	0.1525
Jump frequency vs. max jump	A	-0.0052	0.2775	0.1542
	B	-0.0068	0.3976	0.0485

DISCUSSION

Effects of Morphology and Performance on Behavior

There do not appear to be any significant correlations between morphology, as measured by SVL and hindlimb length, and the amount of time a lizard spends moving in two undisturbed, perch-rich habitats or the frequency of jumps it makes in those habitats. A lizard's maximum jumping capacity, regardless of its morphology, also does not appear to affect its undisturbed behavior. Though the lines of best fit have slight positive or negative slopes for each pairing, the R square values are too small to be considered significant. These results may stem from the lack of correlation between hindlimb length and maximum jump distance in the set of lizards used in this study. Previous work has shown clearly that limb length has a significant effect on maximum jump performance in *Anolis* lizards (Toro et al. 2003). The lack of such a finding in these studies suggest either too small a size range among lizards, or an inability to elicit "true" maximal performances.

As mentioned previously, Garland Jr. et al. (1990) showed that there was no correlation between maximal performance and behavior in *A. lineatopus* and *A. gundlachi* since lizards often use submaximal locomotion during their regular behaviors. They concluded that performance does not limit these lizards'

behavior. This observation held true in this study since neither maximum jumping capacity nor hindlimb length, which have been shown to be an indicator of locomotor capacity, were correlated with jump frequencies or the amount of time lizards spent moving in their habitat.

The data set collected on the average jump distances lizards made was not useful, particularly given that some jumps were of an unknown distance. The majority of jumps made by lizards were to an adjacent perch, so it appears that lizards tend to make short distance jumps to reach a destination when they can. This supports the conclusion that lizards use submaximal locomotion more often than they use maximal locomotion, so their typical behaviors would not necessarily be limited by their maximal performance capacities.

Effects of Perch Density

The average percent of time animals spent moving was higher in setup A than in setup B, whereas the reverse was true for jump frequency. The P values for the paired t-tests were low, but statistically insignificant, and more data should be gathered before drawing any conclusions regarding the effects of perch density on locomotor behavior.

Assuming that the collection of more data leads to statistical significance, conclusions can be drawn about differences in locomotor behavior of *A. carolinensis* individuals in habitats of different perch densities. It appears that lizards will jump more frequently in habitats of high perch density than in habitats

of low perch density (Irschick et al. 2000, Moermond 1979, Pounds 1988). Since the reverse is true for the percent of time individuals spend walking or running through their habitats, it seems that lizards make tradeoffs between jumping and other locomotor modes as perch density changes. Perhaps jumping long distances is more energetically costly than walking or running. Jumping long distances unnecessarily may also expose lizards to predators, especially in habitats of low perch density, so lizards resort to safer modes of locomotion (Bels et al. 1992). However, more data should be collected regarding the effects of perch density on behavior before these assumptions can be accepted as plausible.

CHAPTER 2

THE EFFECTS OF CAUDAL AUTOTOMY ON JUMPING PERFORMANCE

INTRODUCTION

Autotomy, or the self-amputation of an appendage, is a strategy used to escape predators throughout the animal kingdom. Groups that use autotomy include, but are not limited to, numerous invertebrates (e.g. molluscs, crustaceans, starfish, spiders) (Langkilde et al. 2005), salamanders (Kelehear and Webb 2006, Langkilde et al. 2005), rodents (Kelehear and Webb 2006), snakes (Downes and Shine 2001), and lizards (Etheridge 1967). Caudal autotomy, or tail loss, is used in 13 of the approximately 20 lizard families as a defensive strategy (Downes and Shine 2001). Lizards typically try other anti-predator tactics, such as crypsis, fleeing, biting, and defecation, before resorting to caudal autotomy (Brown et al. 1995), but in potentially fatal situations, the lizard can sacrifice its tail to escape a predator's grasp. When a lizard's tail is autotomized, muscles involved in its bending remain active (Rumping and Jayne 1996) and the tail may thrash vigorously, often distracting a predator long enough to allow the individual to escape (Meyer et al. 2002, Naya et al. 2007). Tail thrashing is normally only found in species that use autotomy as a primary escape mechanism (Naya et al. 2007).

Caudal autotomy in lizards is facilitated by autotomic planes of fracture, which are located in caudal vertebrae (Etheridge 1967). The fracture planes are formed by cartilage or connective tissue and pass through the centrum and part or all of the neural arch (Etheridge 1967). The cartilage or connective tissue develops after ossification has taken place, either late in embryonic development or post-embryonically (Etheridge 1967). As in most tailed animals, caudal vertebrae in lizards change gradually from the body to the tail tip. In all lizards the first few caudal vertebrae have only one pair of transverse processes and lack autotomic planes of fracture (Etheridge 1967). In the family Iguanidae, which includes the genus *Anolis*, individuals have long tails, which begin with the non-autotomic vertebrae followed by many vertebrae without transverse processes (Etheridge 1967).

Connective tissues, muscles, and blood vessels are also modified for autotomy (Etheridge 1967) and tail regeneration. These modifications facilitate the release of the tail as the vertebrae are broken while causing minimal damage to the individual. There is no evidence showing that locomotor muscles located in or around the tail are damaged enough to reduce locomotor performance (Chapple and Swain 2002). Regenerated sections of tail cannot be autotomized because true autotomy in lizards can only occur at a plane of fracture (Meyer et al. 2002), and the regenerated portion does not have the specialized tissues for autotomy.

Regeneration of the tail usually only occurs if the tail is broken at an autotomic plane, and will not necessarily happen if the tail was broken between

vertebrae (Etheridge 1967). The regenerated tail's morphology differs greatly from the original tail. Instead of being supported by ossified vertebrae, the regenerated portion of tail is supported by a cartilaginous tube (Meyer et al. 2002). The new muscles do not attach to the skeleton and are not as segmentally regular as the muscles in the original tail (Meyer et al. 2002). The muscles are innervated by one of the three distal nerves from the section of original tail (Meyer et al. 2002). Regenerated tails have higher energy content than original tails because of the different tissue types used in their construction (Naya et al. 2007, Vitt et al. 1997). Because of this, and the relatively fast growth rate of regenerated tails, tail regeneration is very energetically costly (Meyer et al. 2002, Naya et al. 2007).

Aside from functioning as an instrument for predator escape, the tail also functions in predator distraction, sexual displays, locomotion (as a balancing or stabilizing organ), and energy storage (Vitt et al. 1977). Since lizard tails have so many functions, the immediate benefits of autotomy are accompanied by many long-term costs, which vary across species. Lizards that use their tails as an organ for lipid storage lose their energy reserves, often resulting in reduced reproductive capacity or decreased growth rates (reviewed in Brown et al. 1995, Chapple and Swain 2002, Kelehear and Webb 2006, Langkilde et al. 2005, Lin and Ji 2005, Meyer et al. 2002, Naya et al. 2007), though partial tail loss may not influence lipid stores significantly (Lin and Ji 2005, Lin et al. 2006). Attempts at winter dormancy have a higher likelihood of failing post-autotomy (Lin et al. 2006), and

social status, particularly in males, may be reduced after autotomy (reviewed in Brown et al. 1995, Chapple and Swain 2002, Kelehear and Webb 2006, Langkilde et al. 2005, Lin and Ji 2005, Meyer et al. 2002, Naya et al. 2007). If enough of the tail is lost, the lizard temporarily loses autotomy as a predator escape strategy (Langkilde et al. 2005).

Tailless lizards may also encounter numerous locomotor costs (reviewed in Brown et al. 1995, Chapple and Swain 2002, Kelehear and Webb 2006, Langkilde et al. 2005, Lin and Ji 2005, Meyer et al. 2002, Naya et al. 2007), which may lead to modified habitat use and activity levels (Chapple and Swain 2002). Reductions in locomotor performance from autotomy may influence individual behavior in response to predation attempts. For example, tailless individuals of some species flee sooner when approached by predators, which may be in response to their reduced performance (Downes and Shine 2001). Kelehear and Webb (2006) hypothesized that individuals change their microhabitat use or anti-predator strategies to offset locomotor costs of autotomy. Individuals of some species do change their anti-predator behaviors by fleeing when a predator is at a greater distance, relying on crypsis more, or defending themselves aggressively when under pressure (reviewed in Garland and Losos 1994, Losos and Irschick 1996). Tailless individuals forage differently, have smaller home ranges, alter their movement patterns and activity levels, and modify their habitat use post-autotomy (reviewed in Naya et al. 2007). Some of these behavioral changes can reduce individual fitness (Chapple and Swain 2002).

Locomotor costs are diverse and vary across species. Partial tail loss may not have a significant effect on locomotor performance (Lin and Ji 2005, Lin et al 2006), and some species do not experience any reduction in locomotor performance (reviewed in Chapple and Swain 2002, Kelehear and Webb 2006). The effect of autotomy on locomotion is dependent on the function of the tail during locomotion. Tail loss can reduce maximal sprint speeds in many species (Goodman 2006, Lin et al. 2006, Punzo 1982), particularly those that use their tails as a counterbalance in bipedal locomotion (Ballinger et al. 1979). Arboreal lizards tend to use their tails to balance themselves during climbing (Ballinger 1973), and climbing speed may suffer as a result of autotomy (Brown et al. 1995). Unspecialized climbers use their tails to distribute their weight on grasses, leaves, and other flimsy vegetation (Arnold 1988, Sinervo and Losos 1991). Stride length during sprinting post-autotomy is reduced in some species (Martin and Avery 1998), thereby reducing sprint speed or making high sprint speeds more energetically costly. Although sprint speeds may not be significantly affected in all species, their sprinting behavior may change, and some species pause more often during sprinting post-autotomy (Lin and Ji 2005). In some species, individuals with regenerated tails respond differently to autotomy, which indicates that individuals become familiarized with or learn to deal with the costs of autotomy (Brown et al. 1995).

Despite the prevalence of jumping as a form of locomotion in lizards, little is known about how autotomy affects jumping behavior. Thus, I chose to study

the effects of caudal autotomy on jumping in *Anolis carolinensis*, which are known to use their tails as a balancing organ for arboreal locomotion (Ballinger 1973, reviewed in Vitt et al. 1977). Takeoff angles in maximal distance jumps in this species are relatively constant, and the lizards maintain a relatively constant body angle during jumping (Bels et al. 1992, Toro et al. 2004). I hypothesized that *A. carolinensis* use their tails for balance and control during the flight phase of jumping (see Introduction in Chapter 2 for a description of jump phases), and therefore body angles will be more variable during flight post-autotomy, likely reducing landing coordination and possibly influencing jump distance.

METHODS

Animals

Four healthy, wild-caught *A. carolinensis* with completely original tails were purchased from Dave's Soda and Pet City in Hadley, MA. All individuals were kept at Mount Holyoke College in a temperature-controlled room maintained at 20°C. Lizards were housed in pairs in 10-gallon glass terraria, bedded with carpet and furnished with plastic leaves. Tanks were moistened at least twice every day, and lizards were fed 4-6 mealworms each 2-3 times per week.

Jumping Performance and Body Angles

A Photron 1280 PCI high-speed video camera was used to record maximum jump distances from each individual before performing autotomy. Jumps were performed in the same arena described in the Materials and Methods section of Chapter 1. Each video was recorded from a dorsal view at either 250 or 500 frames per second (fps). The pectoral girdle, center of the trunk, pelvic girdle, and a proximal portion of the tail of each individual were marked with white-out paint before jumping trials began. Lizards were encouraged to jump by touching

their tails or toes until jump initiation. Jumps were only recorded if they had a fairly straight trajectory. Three to five videos were recorded of each lizard jumping before inducing autotomy.

Videos were reviewed and the horizontal distance traveled by individuals during jumps was determined. The times of the following events were recorded from each video as well: the initiation of a jump (when the lizard's body began to move forward), the moment of takeoff (the first frame in which the lizard loses contact with the substrate), hindlimb landing, and forelimb landing. Three to four videos were selected based on whether the lizard's body twisted during the jump, video quality, and if the jumps were close to the maximum jump distance. These videos were broken down into their individual images in a TIFF format and every odd frame for videos recorded at 250 fps, and every fourth frame for videos recorded at 500 fps were saved. These TIFF files were imported into the software program Didge (Courtesy of Alistair Cullum, Creighton University) and the coordinates of the lizards' snout, pectoral girdle, trunk, pelvic girdle, and tail were digitized throughout the jump. Using the coordinates of the pectoral and pelvic girdles, the lizards' body angle relative to the horizontal was determined throughout the jump.

Immediately after these jumping trials, all animals' tails were autotomized. Before inducing autotomy, each individual's SVL, tail length, and mass were measured. To induce autotomy, the lizards' tails were grasped

approximately 1 cm posterior to the vent with forceps. The lizard was allowed to hold onto a substrate and was gently shaken until autotomy occurred.

Following autotomy, jump recordings were repeated in the same manner as before autotomy to avoid allowing the lizard to learn to adjust to tailless jumping. Three to ten videos were then recorded of each lizard jumping post-autotomy and two to four were selected for analysis. The same analysis of body angles was performed as for pre-autotomy jumps.

Data analysis

Average body angles and their standard deviations and standard errors were calculated at jump initiation, takeoff, 25%, 50%, 75% and 100% through flight. Body angles for all jumps were plotted against jump stage to qualitatively observe variation in body angles pre- and post-autotomy. Standard deviations from takeoff through landing for both pre- and post-autotomy jumps were plotted, and linear regression was performed on each data set to calculate changes in body angle variation throughout flight.

A paired two-sample t-test was performed on the average jump distances of all individuals before and after autotomy. Two-sample t-test assuming unequal variance was performed on the average jump distances within each lizard to determine if jump distances were significantly different before and after autotomy. These data were compared to individual trends in post-autotomy body angles to determine if body angles were affected by jump distance.

RESULTS

Pre-autotomy body angles

Before autotomy, all lizards jumped similarly, maintaining their bodies slightly above the horizontal plane from take-off to landing (e.g., Figure 2.1). Average body angles and their standard deviations and standard errors at defined reference points throughout a jump are shown in Table 2.1. Body angles at initiation were on average slightly negative, but increased to a positive angle by takeoff. In some cases, high-speed videos of jumping show the lizard's tail being raised if its body angle increased, followed by a decrease in body angle. However, the tail movements were not quantified systematically in this experiment.

Post-autotomy body angles

Individuals responded differently to autotomy. The body angle of 2 animals post-autotomy increased to a maximum angle of 70.9° (Figure 2.2). One of those lizards also made shorter jumps with its body oriented with a negative angle to the horizontal, though those jumps were not included in this quantitative analysis. One individual consistently jumped with its body at a negative angle from initiation through landing (Figure 2.3). Another lizard consistently jumped

with both slight positive and negative angles near the horizontal. Average body angles and their variability at defined reference points throughout a jump are shown in Table 2.2. In some of the jumps with large body angles during flight, lizards appear as though they are attempting to raise their tail to balance themselves, but these movements were not systematically quantified in this experiment.

Jump distances

Pre-autotomy jumps averaged 25.5 ± 2.3 cm and were slightly longer than post-autotomy jumps, which averaged 22.5 ± 1.9 cm. These differences were close to statistical significance ($P = 0.059$). Among the four individuals, two of the lizards had significantly different pre- and post-autotomy jump distances, whereas the other two did not (Table 2.3). Those lizards with significantly shorter jump distances post-autotomy were the lizards that jumped with nearly horizontal or negative body angles.

Effects of autotomy

The body angles at each stage of the jump for all jumps from all lizards before and after autotomy are shown in Figure 2.4. Pre-autotomy body angles remain clumped across all jumps, reflecting the maintenance of a consistently small and positive angle to the horizontal. However, post-autotomy, the body angles are clumped at jump initiation, like the pre-autotomy jumps, but body

angles become more variable as the jump progresses. Some post-autotomy body angles remain within the range of pre-autotomy body angles, and the mean body angles at different jump stages remain approximately equal. Post-autotomy standard deviations during flight increased linearly during the duration of flight ($R^2 = .975$) (Figure 2.5).

Table 2.1. Average body angles (degrees) at jump initiation, takeoff, 25% intervals throughout flight, and landing pre-autotomy.

Pre-autotomy						
	Initiation	Take-off	25%	50%	75%	Landing
Average body angle	-5.630	14.966	16.009	13.469	11.418	8.028
Standard deviation	5.425	7.638	9.610	8.456	7.795	6.050
Standard error	1.505	2.118	2.665	2.345	2.162	1.678

Table 2.2. Average body angles (degrees) at jump initiation, takeoff, 25% intervals throughout flight, and landing post-autotomy.

Post-autotomy						
	Initiation	Take-off	25%	50%	75%	Landing
Average body angle	-5.677	4.953	11.466	17.678	22.268	25.853
Standard deviation	6.695	14.399	18.093	22.980	28.535	29.846
Standard error	1.789	3.848	4.835	6.142	7.626	7.977

Table 2.3. Average pre- and post-autotomy jump distances, two-sample t-test P values and post-autotomy body angle trends for each individual.

Lizard	Pre-autotomy jump distance	Post-autotomy jump distance	P-value	Post-autotomy angles
2	28.3 cm (3)	19.0 cm (2)	0.028	Negative
3	26.3 cm (3)	26.9 cm (4)	0.378	Positive
5	31.1 cm (4)	23.5 cm (4)	0.003	Negative
11	25.5 cm (3)	22.5 cm (4)	0.08	Positive

Number of samples used to calculate mean jump distances are in parentheses

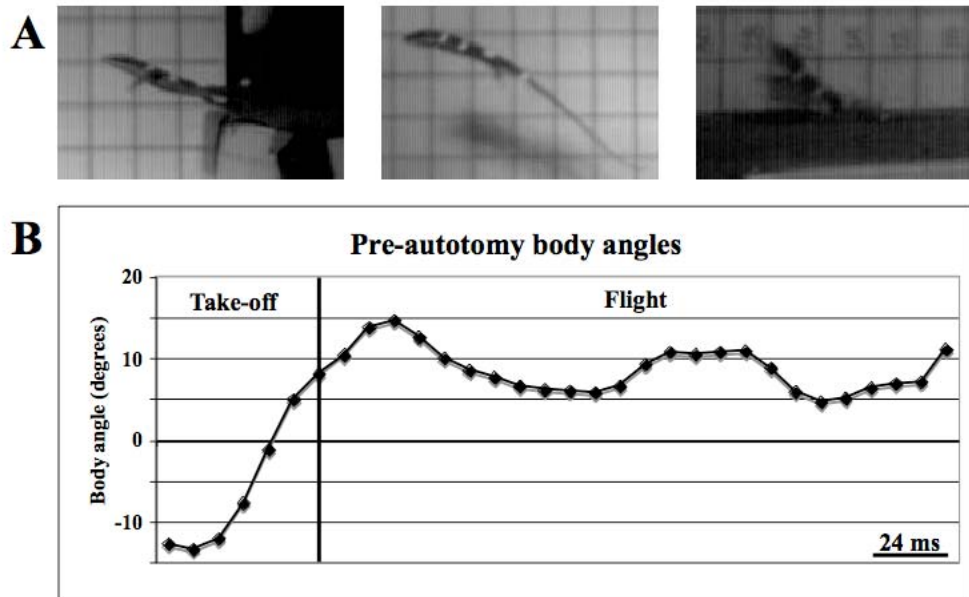


Figure 2.1. (A) Frames taken from high-speed videos of a pre-autotomy jump at take-off, mid-flight, and landing. (B) The changes in body angle throughout one pre-autotomy jump from initiation through landing. Note that following takeoff, the body subtends a small but consistently positive angle relative to the horizontal until landing.

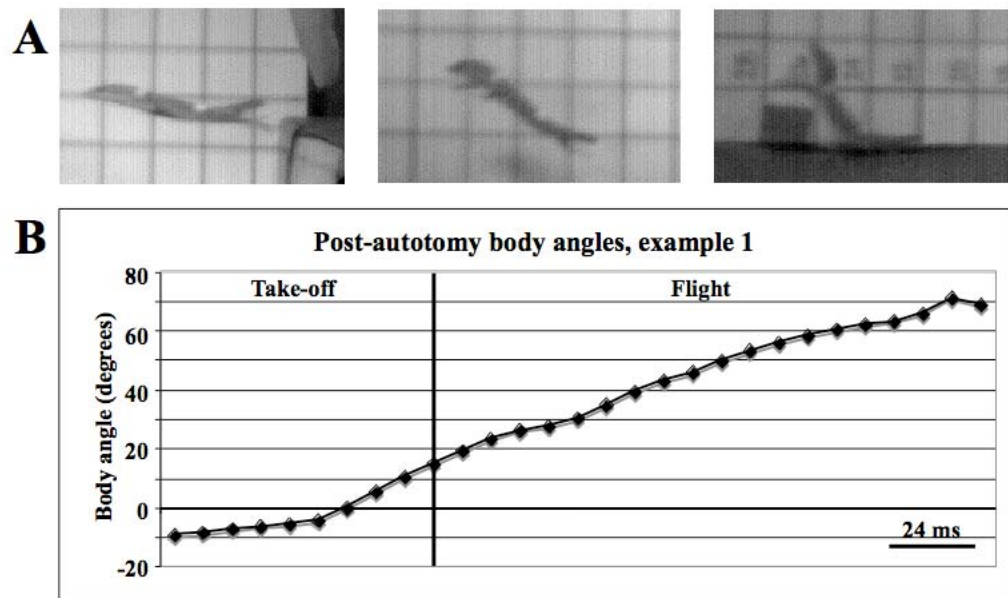


Figure 2.2. (A) Frames taken from high-speed videos of a post-autotomy jump at take-off, mid-flight, and landing. (B) The changes in body angle throughout a post-autotomy jump highlighting the continuous clockwise rotation of the animal's body throughout the flight phase, leading to extremely high body angle values at landing relative to pre-autotomy jumps.

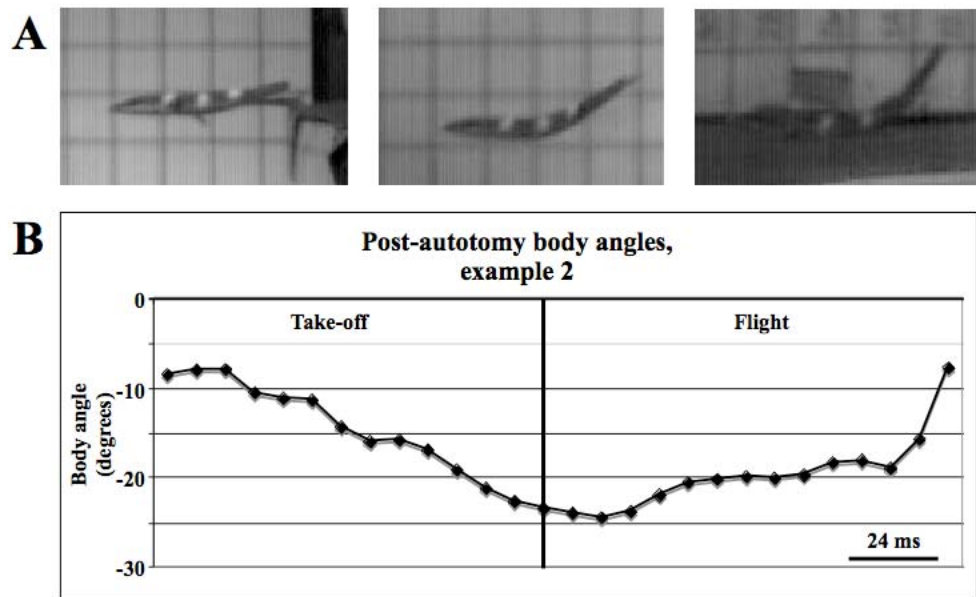


Figure 2.3. (A) Frames taken from high-speed videos of a post-autotomy jump at take-off, mid-flight, and landing. (B) The changes in body angle throughout a post-autotomy jump. Note that all body angle values are negative.

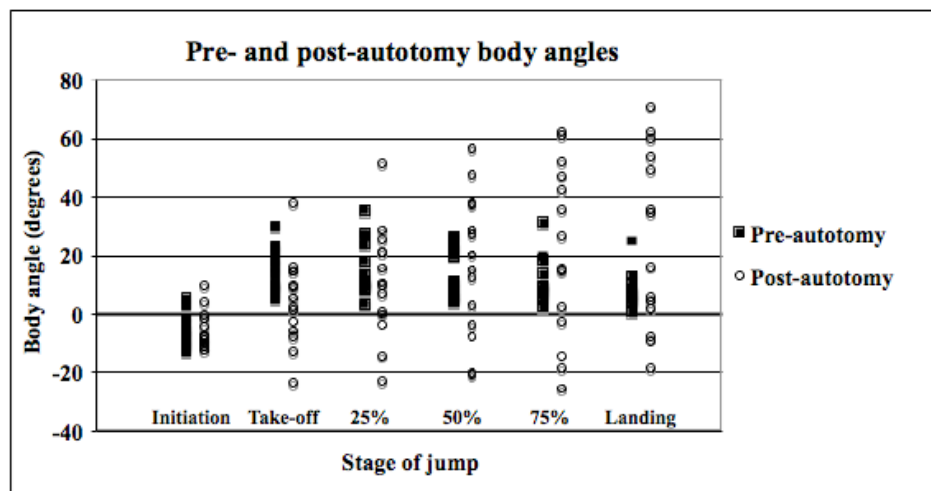


Figure 2.4. Body angle values from each jump pre- and post-autotomy plotted against jump stage. Note the increased variability in post-autotomy jumps as the flight phase progresses.

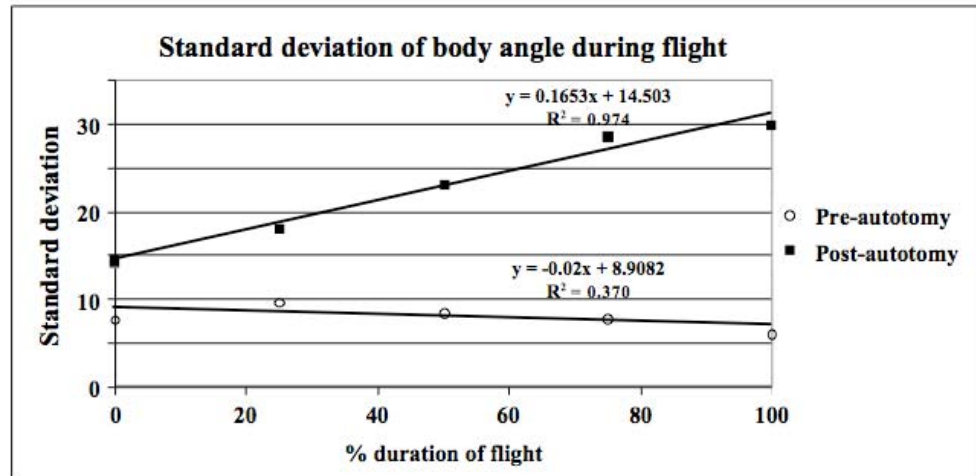


Figure 2.5. Standard deviations of average body angles from takeoff (0% flight) to landing (100% flight) pre- and post-autotomy and the linear regressions to fit the data sets. Standard deviations, and hence variation increase consistently throughout post-autotomy jumps.

DISCUSSION

Tail use during jumping

The data from these experiments suggest that *A. carolinensis* probably rely on their tails to control their body position during jumping. Pre-autotomy body angles during flight are nearly constant and fairly consistent across individuals. The increase in variation of body angles during flight post-autotomy supports the conclusion that the presence of a tail helps a lizard control its body angle during flight and landing. The observations that some lizards raise their tails during jumps pre-autotomy and attempt to do so post-autotomy also imply that lizards use their tails in flight during jumping. Unfortunately, this experiment did not include quantification of tail movements (or attempts at tail movements) during jumping, but future studies of tail function in flight should include analysis of the relationship between tail movements and body angle changes during jumping. Further, experiments in which different amounts of tail are removed, or weights are added to the tail might also help illuminate the importance of tail movement for achieving body coordination in jumps.

Jump distance

Numerous studies have examined the effects of caudal autotomy on sprinting performance (Ballinger et al. 1979, Goodman 2006, Lin et al. 2006, Martin and Avery 1998, Punzo 1982) and climbing performance (Arnold 1988, Ballinger 1973, Brown et al. 1995, Sinervo and Losos 1991). Though the jump distances across all individuals were not significantly shorter post-autotomy in this experiment, the difference was close to statistical significance. Expansion of the data set using more individuals might reveal a significant difference in jump distances pre- and post-autotomy. This conclusion would add yet another potential locomotor cost of caudal autotomy in lizards, particularly in species that use jumping frequently as a form of locomotion.

Jump distance and body angle

There appears to be a tradeoff between jump distance and body angle during flight. When lizards made jumps of similar distances pre- and post-autotomy, their post-autotomy body angles increased throughout flight. Post-autotomy jumps with negative body angles tended to be shorter than pre-autotomy jumps in the same individual. This suggests that some lizards may modify their jumping behavior post-autotomy to control their body during jumping to control landings and jump distances. By taking off with a negative body angle, lizards reduce their jump distance, but land at an angle similar to their pre-autotomy

landing angles. The behavioral change results in an increase in coordination at the cost of reduced jump distance.

The difference in body angles post-autotomy may be a function of force output and takeoff angle. Pre-autotomy jump distances are positively correlated with force output at takeoff (Biewener 2003, Toro et al. 2006), and the relationship presumably holds true post-autotomy. In addition to jump distance, post-autotomy body angles may be affected by force output at takeoff. Future studies should examine the relationships between post-autotomy force output at takeoff, takeoff angles, and body angles during jumping to test these hypotheses and determine the causes of the variation in body angles post-autotomy.

Effects of autotomy on behavior and fitness

As previously mentioned, some species of lizards alter their escape behavior and habitat use after tail loss (Downes and Shine 2001, Garland and Losos 1994, Greene 1988, Kelehear and Webb 2006, Losos and Irschick 1996, reviewed in Naya et al. 2007). Similar autotomy-induced behavioral effects might also be present in *A. carolinensis*. Two lizards, which were not included in this study, refused to jump under post-autotomy experimental conditions. Instead of jumping when disturbed, they tended to remain motionless and/or sprint across the platform. This behavior could be due to stress caused by autotomy, the experimental conditions, or a behavioral response in an attempt to increase survival probabilities during predatory attacks. Individuals may alter their

behavior post-autotomy to avoid using locomotor activities that have been significantly compromised following tail loss.

Changes in locomotor capacity and behavior post-autotomy can reduce survival and fitness in some species of lizards (Chapple and Swain 2002).

Reduction in coordination of body angles during flight and landing in *A.*

carolinensis may also lead to lowered fitness and survivorship following tail loss.

Anoles are known to jump to and from small tree branches. If body coordination is reduced in-flight, animals may have a more difficult time landing successfully on a small structure like a branch or twig, and thus may be limited in where they can jump successfully and may end up on the ground after an unsuccessful landing.

In summary, the immediate benefits of caudal autotomy are often accompanied by locomotor costs. This has shown to be true during sprinting (Ballinger et al. 1979, Goodman 2006, Lin et al. 2006, Martin and Avery 1998, Punzo 1982) and climbing (Arnold 1988, Ballinger 1973, Brown et al. 1995, Sinervo and Losos 1991), and this study suggests it is true during jumping as well. Such costs may lead to reduced survival probabilities if an individual is unable to escape predators, loses social status and/or exhibits reduced reproductive rates because it is unable to defend a territory or attract a mate due to reduced locomotor capacity. Caudal autotomy negatively affects the locomotor capacity of *A. carolinensis*, and may subsequently impact the survivorship and fitness of individuals that undergo tail loss.

SUMMARY AND CONCLUSIONS

In this thesis, I explored the possibilities of relationships between morphology and behavior, habitat and behavior, and caudal autotomy and locomotor performance. I addressed 4 major questions in my studies:

- (1) Do morphological features that affect maximal locomotor performance, such as hindlimb length, affect locomotor behavior in an undisturbed environment?
- (2) Does perch density in a habitat affect locomotor behavior?
- (3) Do lizards use their tails to control their body angles during jumping?
and
- (4) Does caudal autotomy reduce the maximal distance a lizard can jump?

Using *Anolis carolinensis* as my experimental species, I performed two experiments to answer these questions.

I hypothesized that hindlimb length, which may be used as a predictor of maximal jump performance in *A. carolinensis*, would be a predictor of undisturbed behavior in a controlled matrix of perches. However, neither the percent of time a lizard spent moving nor the frequency of jumps it made over a three-hour period were correlated with hindlimb length. In addition, maximum jump distances were also unrelated to hindlimb length among individuals used in

this study. Thus, I concluded that neither maximal performance nor the morphological features that I measured affect the locomotor behavior of *A. carolinensis* lizards in the artificial habitats I constructed.

I also hypothesized that lizards would move through their environment more if perches were present in a higher density. The results from this portion of the study were close to significant, but require more data collection to determine whether perch density has an effect on locomotor behavior. Currently, results suggest, but do not clearly demonstrate, that lizards walk or run for a larger percent of time in habitats with a low perch density, and jump more frequently in habitats with a high perch density.

For the tail autotomy experiments, I predicted that *A. carolinensis* lizards use their tails for body control during jumping. My data support this hypothesis, since body angle variation in-flight is generally greater in lizards post-autotomy, and also increases throughout a jump. In addition, qualitative observations of tail movements suggest that lizards may lift their tails during jumps to stabilize their body angle. Future studies should attempt to quantify tail movements to determine their effect on body angles during jumping.

My final hypothesis was that the loss of control of body angles during jumping post-autotomy would result in a reduction of maximal jump distance. At this point, this hypothesis is rejected, as differences in maximal distance between pre-and post-autotomy jumps were not quite significant. However, the trend for post-autotomy jumps to be shorter was clear in two of four lizards, and more

individuals need to be tested before more firm conclusions can be drawn. In the two individuals for which jump distances were not significantly different before and after tail loss, body angles were larger post-autotomy. In the other two individuals in which autotomy appeared to affect maximum jump distances, body angles during jumping tended to be near or below the horizontal plane after autotomy. Future studies should examine the effects of caudal autotomy on jumping further by studying the relationships between force output and takeoff angle, which affect jump distance, and body angles during jumping post-autotomy.

In summary, I found that the locomotor behavior of *A. carolinensis* lizards may not be affected by maximal performance or the morphological features that predict maximal locomotor performance. However, more data should be collected to verify this conclusion. Perch density had a nearly significant effect on locomotor behavior in this study, but until more data are collected I cannot conclude that perch density affects behavior. Caudal autotomy has a significant effect on body angles during jumping, suggesting that *A. carolinensis* lizards use their tails for stabilization in flight.

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