



## SYMPOSIUM

# Tail Autotomy Alters Prey Capture Performance and Kinematics, but not Success, in Banded Geckos

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**Synopsis** Tails are versatile structures with diverse forms and functions across vertebrates. They are involved in almost all behaviors critical to survival including locomotion, feeding, and predator avoidance. Although the tail's role in locomotion and stability has been widely studied, its role in prey capture is relatively unknown. Lizards are an ideal system to examine the tail's impact on prey capture as most are capable of autotomizing, or dropping, their tail in response to predation and intraspecific competition. Tail autotomy can lower reproduction, decrease locomotor performance, impart instability during jumping, and decrease social status. Desert banded geckos (*Coleonyx variegatus*) frequently capture evasive prey in nature and appear to use their tail during strikes. However, it is unclear if these tail movements are important for the strike itself, or if they simply draw attention to that part of the body. We used high-speed 3D videography to quantify prey capture performance and kinematics of *C. variegatus* striking at crickets before and after total caudal autotomy. Trials were conducted within 2 h of autotomy and then repeatedly over a 2-week period. Overall, prey capture success was unaffected by caudal autotomy. However, maximum strike velocity decreased significantly after autotomy, highlighting the importance of the tail during prey capture. Strike kinematics were altered after autotomy in several ways, including geckos adopting a more sprawled posture. Maximum pectoral girdle and mid-back height were significantly lower during post-autotomy strikes, whereas maximum pelvic girdle height was unaffected. However, individual variation was considerable. This downward pitching of the body after tail loss suggests that the tail is necessary for counterbalancing the anterior portion of the body and resisting the rotational inertia incurred after pushing off with the hindlimbs. Utilizing autotomy to test tail function in prey capture can provide valuable insight into how the tail is used in terrestrial predation across a wide variety of species and ecological niches.

## Introduction

The presence of a post-anal tail is one of the few synapomorphies that define the chordate phylum. While it is lost in some adult chordates, many have specialized tails to assist in a wide variety of functions including swimming (Bartholomew et al. 1976; Graham et al. 1987), gliding (Norberg 1985; Clark et al. 2021), running (Gillis and Higham 2016; Jagnandan and Higham 2017), climbing (Jusufi et al. 2008; Herrel et al. 2013), feeding (Garber and Rehg 1999), gripping (Porter et al. 2015), defense (Greene 1973; Wagner et al. 2013), and sexual display (Gilbert et al. 2020). These specialized functions

are often accompanied by morphological changes, such as modified caudal vertebrae in prehensile tails (e.g., arboreal chameleons; Luger et al. 2020), paddle-shaped tails in sea snakes (Graham et al. 1987), square tails used for gripping in seahorses (Porter et al. 2015), or dorso-ventrally flattened tails in gliding animals (Norberg 1985). Some species even have tails that have adhesive structures (Bauer 1998). Despite the myriad functions and specializations, the specific function of the tail is often difficult to tease apart from the rest of the body.

Tails are important for many behaviors critical to an organism's survival, but one behavior that

remains understudied is the role of the tail in prey capture (Gillis and Higham 2016). Because the tail is integral to locomotion in fishes (Webb 1984) and birds (Thomas 1993), it is almost always used during prey capture that involves predatory movements in these groups. However, in this article, we focus on the tail as a post-anal extension of the spine and associated tissues, excluding structures such as caudal fins or tail feathers. A variety of studies have linked tail use to locomotion (Siegel 1970; Wada et al. 1993; Fleming et al. 2009) and locomotor ability to prey capture success (Higham 2007). However, research on the direct link between tail use and prey capture is limited. Previous studies found tail movements are essential to the rapid high-speed maneuvers used by cheetahs to capture prey (Wilson et al. 2013; Patel et al. 2016), directly used to capture insects mid-flight in bats (Kalko 1995), and used as lures to attract or distract prey in a variety of snake species (Neill 1960), most dramatically the spider-tailed viper, *Pseudocerastes urarachnoides* (Bostanchi et al. 2006). However, these specialized uses do little to elucidate the mechanical role that the tail plays in prey capture strikes.

One challenge in studying the role of the tail in behaviors such as prey capture is the inability to test an animal with and without the tail. The removal of most vertebrate tails is damaging and rarely occurs in nature. Other mechanisms of altering tail function include tail restriction (Jagnandan and Higham 2017), although this is not always feasible. However, some animals are able to shed their tail naturally. Autotomy is the voluntary severance of an organ in response to external pressures (Bateman and Fleming 2009; Higham et al. 2013). This pressure is most often associated with predator avoidance, but can also occur during the intraspecific competition (Arnold 1984). Autotomy has evolved in many invertebrate phyla, as well as amphibians, squamate reptiles, and a few species of rodents (Seifert et al. 2012; Emberts et al. 2019). Caudal autotomy is present in 13 of the 20 lizard families, including the two largest families, the geckos and skinks (Downes and Shine 2001), and is often followed by rapid tail regeneration (Clause and Capaldi 2006). There are numerous consequences of tail autotomy in lizards, ranging from behavioral shifts to changes in performance and stability (Jusufi et al. 2011; McElroy and Bergmann 2013; Lin et al. 2017; Kuo et al. 2019).

In a study of *Psammotromus algirus* lizards, individuals without their tails had a greater latency to attack prey and spent comparatively less time foraging (Martin and Avery 1997, see also Cooper 2003).

However, these studies focus on lizard foraging behavior leading up to prey capture attempts, rather than the use of the tail in prey capture strikes. Lizards have become a model system for prey capture studies (reviewed in Schwenk 2000; Bels et al. 2019; Montuelle and Kane 2019), and recent work found that the strike velocity, which is initiated by the locomotor system, can be quite high (Montuelle et al. 2009, 2012). Thus, it is clear that the postcranial system is critical for accelerating the lizard toward evasive prey. Lizards are ideal for examining the role of the tail in prey capture given their ability to naturally shed their tails and the fact that they occupy a variety of ecological niches and consume a wide array of prey types.

We examined the effects of tail autotomy on the prey capture dynamics of the western banded gecko, *Coleonyx variegatus*. *Coleonyx variegatus* was chosen for this study for their large, active tails, and their diverse diet of evasive invertebrates, including scorpions, coleopterans, orthopterans, and isopterans (Parker and Pianka 1974). In one population of *C. variegatus*, 74% of adults had either missing or regenerated tails, indicating natural rates of tail autotomy are quite high (Parker 1972). While *C. variegatus* tails are quick to regenerate, the majority of adults must capture food without a tail at some point in their life, making the question of how tail autotomy affects prey capture ability highly ecologically relevant.

We used 3D high-speed videography to assess the motions and performance of geckos attacking crickets, a natural prey item, before and after tail autotomy. We predicted that geckos would exhibit a reduction in stability, potentially reducing strike accuracy and capture success. Additionally, we predicted that strike velocity and acceleration would decrease following autotomy. A reduction in locomotor performance is often observed in lizards following autotomy (McElroy and Bergmann 2013), indicating that it may serve as a counterbalance that positions the center of mass closer to the hind limbs. We predict that this may also be important for lunging at prey, thereby decreasing performance following the tail loss.

## Methods

### Collection and animal care

Five juvenile (one female and four male) *C. variegatus* individuals were collected from the Motte Rimrock Reserve in Perris, California in October 2019. Two individuals had regenerated tail tips but were included as the small amount of regenerated

tail did not impact tail mobility. Geckos were kept in separate tanks at a room temperature between 18.3 and 24.8°C, with either incandescent lights or heat pads for a basking spot. Geckos were fed a mixture of live crickets and mealworms and provided water *ad libitum*, but were fasted for 48 h before trials. At the time of testing, the five individuals ranged from 3.23 to 4.03 g in body mass and 48.94 to 56.91 mm in snout–vent length.

### Prey capture trials

Custom experimental arenas (35.60×15.25×15.25 cm) were constructed out of sheets of transparent acrylic. The bottoms of the tanks were lined with a thin layer of cork to provide traction. Dots of white nail polish were painted to mark the head and the approximate location of the center of the pectoral and pelvic girdles, and the midpoint of the back (Fig. 1) for video digitization. Before trials, the geckos were moved to the testing location and given ~24 h to acclimate. Trials were conducted in a dark room between 0.71 and 1.2 lux, as quantified using an illuminance meter (Konica Minolta T-10A). A CMVision IR illuminator producing 850 nm light was used to illuminate the trials for the cameras while maintaining a low light level for the geckos. Trials were conducted in the early evening to correspond with the gecko's natural nocturnal activity patterns. Temperatures during trials ranged from 25.2 to 28.8°C.

Two synchronized Edgertronic high-speed cameras (SC1) were positioned to capture the dorsal and lateral view of the focal arena. The cameras were set to record the 5 s before being triggered and recorded at 500 frames per second. A single gecko was placed into an experimental arena, and trials began by dropping a single cricket into the arena. The cricket was placed away from the gecko, and the gecko would often immediately pursue prey items once detected. Approximately 5 min after consumption, another cricket was placed in the tank until the gecko no longer pursued the prey item.

A minimum of 24 h after at least three successful and three unsuccessful strikes were recorded, gecko tails were fully autotomized by pinching the base of the tail (Jagnandan and Higham 2018a). The geckos were tested again using the same procedure described above 2 h after autotomy, 1 day after autotomy, and every other day afterwards for 2 weeks. It should be noted that the geckos appeared eager to eat immediately after autotomy, sometimes approaching their autotomized tail as if it were prey.

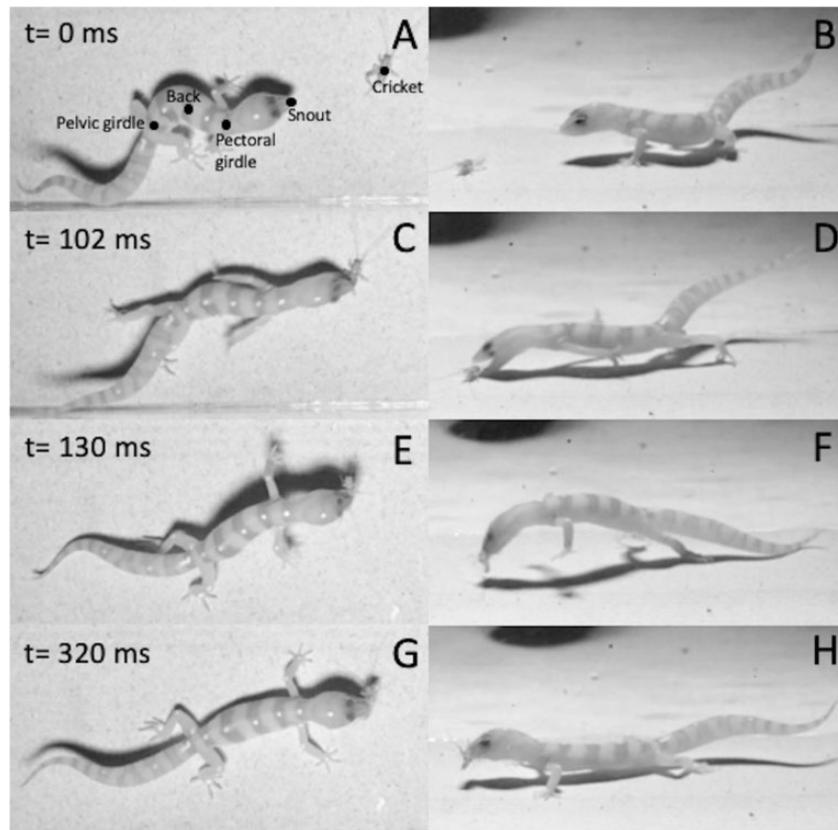
### Video analysis

A pre-measured calibration object comprised of LEGO blocks was used to generate  $x$ ,  $y$ , and  $z$  coordinates for digitizing (Jagnandan and Higham 2018a). Relevant points on the gecko were digitized using the MATLAB DLTdv8 tool (Hedrick 2008). The resulting coordinates were smoothed using a low-pass zero-lag Butterworth filter at 50 HZ (as in Whitford et al. 2019) using a custom MATLAB script. Smoothed snout and cricket points were used to calculate the 3D distance between the gecko and cricket. The snout point was used to quantify gecko velocity and acceleration. Maximum velocity and acceleration for each strike were averaged together by the individual for each treatment (before autotomy, 2 h after, 1 day after, etc.). The pectoral girdle, midpoint of the back, and pelvic girdle points were used to calculate the height of each point throughout the strike by subtracting the smoothed  $z$  coordinate by the  $z$  coordinate of a static point on the substrate surface. The starting heights were calculated immediately before any movement of the gecko. Starting heights of the body points between pre- and post-autotomy strikes were used as a proxy to compare lizard posture with lower heights indicating a more sprawled posture. Maximum height and height at the time of prey capture for each point over the course of the digitized strike were obtained.

We visually inspected each video to determine whether strikes could be accurately digitized and were not impeded. Strikes where the gecko interacted with the wall, where the digitization points were obscured for a significant portion of the strike, or where the gecko contorted its body to strike backward at the target were excluded from analyses.

### Statistics

A Wilcoxon Signed-Rank Test was used to compare the rate of prey capture success between pre- and post-autotomy strikes. Generalized linear mixed models (GLMM) were used to compare maximum velocity, maximum acceleration/deceleration, and the starting, contact, and maximum heights of the pectoral girdle, midpoint of back, and pelvic girdle across pre- and post-autotomy strikes. These GLMMs were performed using the mean value of the individual averages. Individual (random categorical factor) and autotomy (fixed categorical factor) were used as independent variables. Both successful and unsuccessful strikes were included in the analysis as the focus of our study was on the difference between pre- and post-autotomy strikes rather than between successful and unsuccessful strikes. We



**Fig. 1** A representative high-speed sequence (500 frames/s) of pre-autotomy prey capture.  $t = 0$  indicates the onset of strike movement. Points used in digitizing are indicated. Time is in milliseconds. Note the S posture of the body at the beginning of strike movement and the arched back and tail held low to the ground in (F).

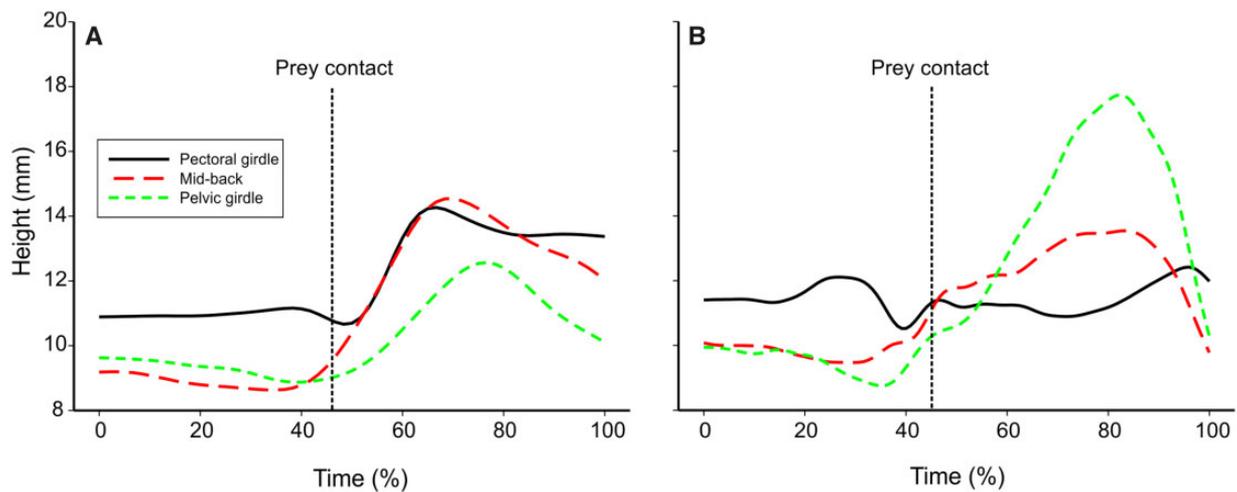
performed linear regressions to determine whether temperature or humidity impacted maximum velocity, as well as to determine whether maximum pelvic girdle height was impacted by maximum acceleration. Calculations were carried out using custom script in RStudio, MATLAB, and SYSTAT.  $P < 0.05$  was used as the criterion for statistical significance.

## Results

Western banded geckos used an active foraging strategy while in the testing arena. Approaches and lunges toward the prey were variable, but strikes generally began with the gecko approaching the prey in a crouched stance, followed by a rapid extension of both the fore- and hindlimbs. Prey contact was initiated by the jaws. After contacting the prey, but prior to landing on the front limbs, geckos typically arched their back and raised their head, and the strike would conclude with all limbs returning to the ground (Fig. 1). Hindlimbs occasionally left the ground, but more often were dragged behind the body as the gecko lunged (Fig. 1). However, a second pattern was also observed, where geckos would initiate strikes closer to the cricket and would only

utilize the front legs, neck, and head to thrust the jaws toward the prey. This second pattern was observed more commonly after autotomy. A final pattern, only observed after autotomy, involved the pelvic girdle and back legs of the geckos leaving the ground and rising above the anterior portion of the body as the gecko made contact with the prey and the front limbs contacted the ground. This resulted in an increased time period after contact where the gecko's back legs were in the air (Fig. 2). This type of strike was observed in 14 of 64 post-autotomy strikes with a high degree of individual variation. In three individuals, this type of strike was mainly observed only within the first day after autotomy, one individual continued to exhibit this pattern throughout the 2 weeks after autotomy, and one individual did not perform this type of strike.

The percentage of successful prey capture strikes was not significantly different between pre- and post-autotomy trials (Wilcoxon signed-rank test,  $w = 7$ ,  $P > 0.10$ ; Fig. 3B). Starting distance to the prey item was also not significantly different post-autotomy (GLMM,  $F_{1,4} = 7.27$ ,  $P = 0.054$ ; Fig. 3E). However, maximum velocity and maximum



**Fig. 2** Height of the pectoral girdle (black solid line), the midpoint of the back (red long dashed line), and pelvic girdle (green short dashed line) over the course of a strike (**A**) where the back legs rise over the body during the trial and (**B**) where the back legs stay low to the ground. The 0% of the strike corresponds with the initiation of movement toward the prey, while 100% of the strike corresponds to the head raised to a resting position with the prey item in the mouth. Both trials were performed on the same day by the same individual, 2 h after autotomy. Note the much higher maximum of the pelvic girdle in (B).

acceleration were both significantly lower post-autotomy (GLMM, velocity:  $F_{1,4} = 13.607$ ,  $P = 0.021$ , acceleration:  $F_{1,4} = 8.446$ ,  $P = 0.044$ ; Fig. 3A and 3C). Maximum deceleration following prey capture was also significantly higher pre-autotomy ( $F_{1,4} = 8.038$ ,  $P = 0.047$ ; Fig. 3D; Table 1). On average, maximum acceleration occurred 16.34 ms before contact (standard deviation =  $\pm 6.71$  ms), maximum velocity occurred 9.03 ms before contact (standard deviation [SD] =  $\pm 5.75$  ms), and maximum deceleration occurred 0.2 ms after contact (SD =  $\pm 5.80$  ms).

The pectoral girdle and back points were significantly lower at the start of the strike post-autotomy while the pelvic girdle point was not significantly changed (GLMM, pectoral girdle:  $F_{1,4} = 10$ ,  $P = 0.034$ , back:  $F_{1,4} = 31.77$ ,  $P = 0.005$ , pelvic girdle:  $F_{1,4} = 0.555$ ,  $P = 0.498$ ; Fig. 4A). The maximum heights of these points over the course of the strike followed a similar pattern, where the pectoral girdle and back maximum heights significantly lower post autotomy, while the pelvic height remained unchanged (GLMM, pectoral girdle:  $F_{1,4} = 16.165$ ,  $P = 0.016$ , back:  $F_{1,4} = 22.249$ ,  $P = 0.009$ , pelvic girdle:  $F_{1,4} = 0.8$ ,  $P = 0.421$ ; Fig. 4C; Table 1). At time of prey contact, the pectoral girdle and midpoint of the back were not significantly different between pre- and post-autotomy trials, but the pelvic girdle point was lower at the time of contact in the post-autotomy trials (GLMM, pectoral girdle:  $F_{1,4} = 0.336$ ,  $P = 0.593$ , back:  $F_{1,4} = 7.137$ ,  $P = 0.056$ , pelvic girdle:  $F_{1,4} = 180.68$ ,  $P < 0.0001$ ; Fig. 4B). We found that maximum acceleration was positively correlated

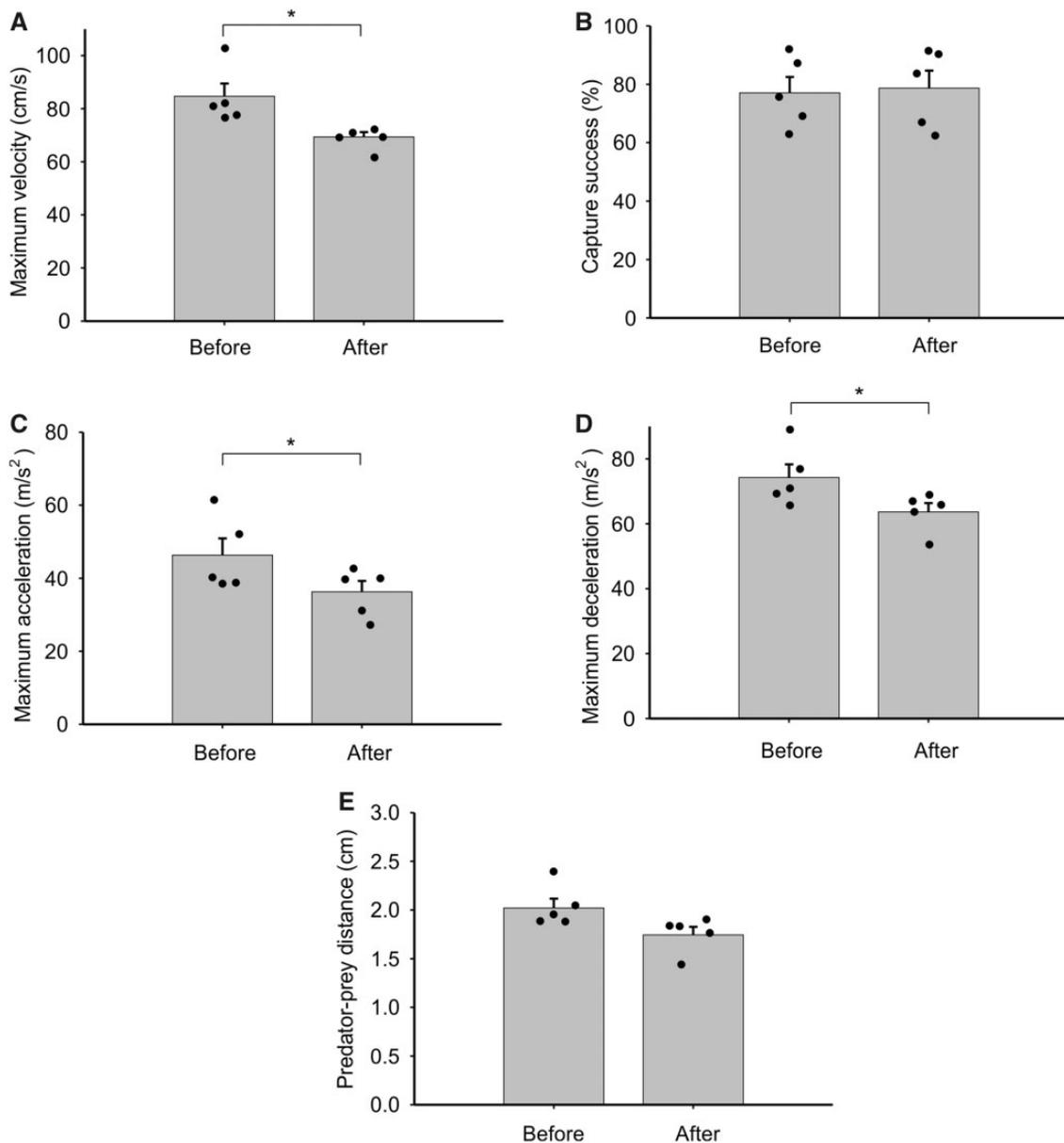
with maximum pelvic girdle height, both before and after autotomy (linear regression;  $P < 0.001$ ; Fig. 5). When trials were separated by gecko, three of the five individuals had a significant positive correlation, while the remaining two had a positive correlation but the linear regression results were not significant.

An analysis of individual variation found the performance variables (maximum velocity, maximum acceleration, etc.) did not vary among individuals, whereas variables associated with the body points had a significant degree of variation between geckos (Fig. 4). However, the response to autotomy was almost always consistent among individuals.

Temperature and humidity had no impact on maximum strike velocity (linear regression, temperature:  $P = 0.34$ , humidity:  $P = 0.45$ ).

## Discussion

Tail autotomy did not impact prey capture success in western banded geckos, but reduced performance and altered kinematics between the pre- and post-autotomy strikes reveal that the tail may be critical for prey capture in nature. The lower starting back height post-autotomy is consistent with previous studies that found geckos adopt a more sprawled stance during locomotion after the loss of the tail (Jagnandan et al. 2014). This posture lowers the center of mass for greater stability and balance (Foster and Higham 2012). The geckos may be adopting this sprawled stance as a necessary adjustment to compensate for the loss of the balance provided by the tail. However, this might be a passive result stemming from the reduced external joint moments



**Fig. 3** Comparison of (A) maximum velocity, (B) capture success, (C) maximum acceleration, (D) maximum deceleration, and (E) starting distance between gecko and cricket between pre- and post-autotomy trials. Points show the average of the variable for each gecko. Individuals were not significantly different, and are therefore all in the same color. Error bars represent standard error of the mean (SEM). Asterisks indicate a  $P < 0.05$ .

associated with a reduction in body mass (see [Jagnandan and Higham 2018b](#) for discussion).

### Strike kinematics

Examining the heights of the body points over the course of a strike supports our hypothesis that the tail is used to control body motion. Tails in other lizard species participate in aerial righting ([Jusufi et al. 2008](#)) and tail loss results in impaired in-air stability, significant body rotation, and increased body

rotation during jumps ([Kuo et al. 2012](#)). We hypothesized that banded geckos might also use their tail for stability and that the loss of the tail would result in less accurate strikes.

All of the body points during the strike varied substantially among individuals. However, some general patterns emerged. On average, maximum hip height (relative to the ground) was not significantly different post-autotomy, but the maximum height relative to the anterior points was greater after tail loss. This downward pitching of the animal after tail

**Table 1** Summary of success, velocity, acceleration, and kinematic variables for pre- and post-autotomy trials

Variables	Pre-autotomy	Post-autotomy
Capture success (%)	77.0	78.6
Starting distance to prey (cm)	2.03 ± 0.08	1.72 ± 0.06
Maximum velocity (cm/s)	85.1 ± 2.19	69.6 ± 1.71*
Maximum acceleration (m/s <sup>2</sup> )	46.6 ± 1.97	37.2 ± 1.73*
Maximum deceleration(m/s <sup>2</sup> )	-74.7 ± 2.54	-64.0 ± 2.38*
Starting pectoral girdle height (mm)	14.2 ± 0.26	13.4 ± 0.26*
Starting midpoint of back height (mm)	12.5 ± 0.22	11.6 ± 0.20*
Starting pelvic girdle height (mm)	10.2 ± 0.15	10.1 ± 0.19
Pectoral girdle height at contact (mm)	13.2 ± 0.23	13.1 ± 0.22
Midpoint of back height at contact (mm)	12.8 ± 0.22	11.9 ± 0.24
Pelvic girdle height at contact (mm)	11.0 ± 0.19	10.1 ± 0.19*
Maximum pectoral girdle height (mm)	16.4 ± 0.32	15.1 ± 0.28*
Maximum midpoint of back height (mm)	16.3 ± 0.43	14.6 ± 0.38*
Maximum pelvic girdle height (mm)	13.5 ± 0.31	13.1 ± 0.39

Values are means ± SEM. Asterisks indicate a  $P < 0.05$  from a generalized linear mixed model.

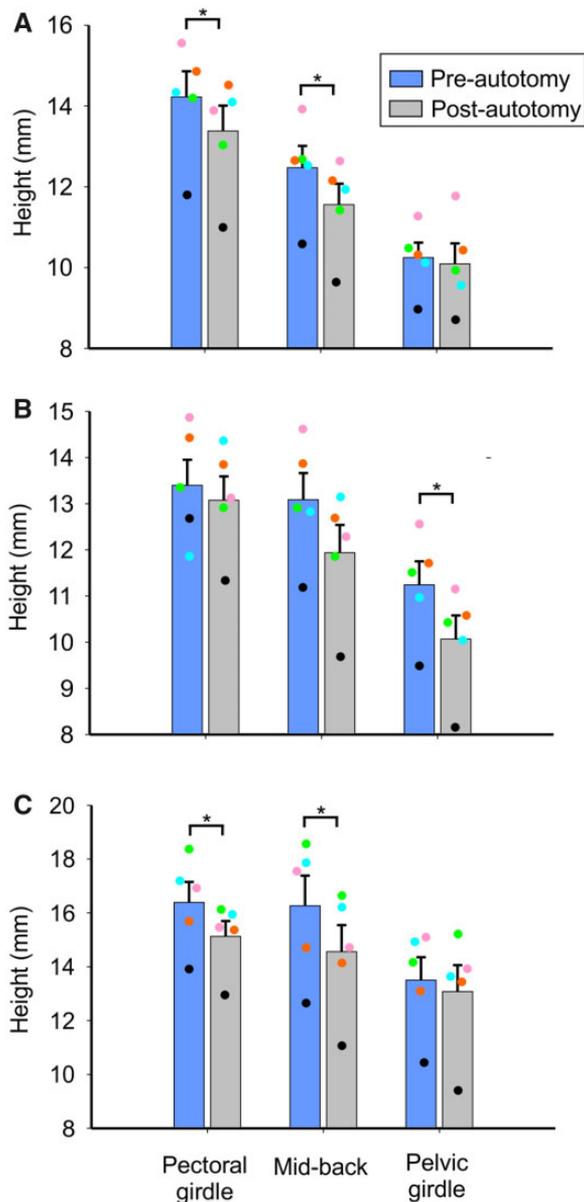
loss implies that the tail is necessary for counterbalancing the anterior portion of the body and resisting the rotational inertia incurred after pushing off with the hindlimbs. This also highlights the consequence of shifting the center of mass forward but keeping the propulsive force in the same location. The rotational moment, or torque, about the center of mass will increase since the ground reactive force (GRF) vector would be more posterior after autotomy relative to pre-autotomy strikes. Future work incorporating inverse dynamics will provide important information about how the application of forces is altered by tail loss, and how much this moment about the center of mass changes.

As noted, each gecko with an intact tail typically had an arched back after contacting the prey, allowing the pelvis and tail to stay low and provide an effective braking mechanism after the strike. Post-autotomy, the back remains in line with the rest of the body. We hypothesize this difference is indicative of how the tail is used during a strike, as a counterweight to control pitch and keep the hip and back legs lower, allowing for more effective braking as the back legs are dragged across the ground (Fig. 1F). This hypothesis is supported by the fact that maximum deceleration is significantly higher pre-autotomy. This may also provide an explanation for why prey capture success was unaffected by autotomy; this difference in strike kinematics only appears after contacting the prey, so if the prey is already in the gecko's mouth, prey capture success is likely unaffected.

### Maximum velocity and acceleration

The loss of the tail resulted in a significant reduction in maximum acceleration, deceleration, and velocity of the strikes (Fig. 3A, C, and D). The sprawled position discussed above may also be contributing to the observed drop in velocity and acceleration. Striking in the lower position would alter the GRF vector to include a more medially directed force (see Russell and Bels, 2001 for review). As a result, the component of the GRF that is directed anteriorly is likely reduced, leading to a decrease in velocity. However, it should be noted that, in addition to the change in posture, the overall body mass, especially in the posterior region, is lower after autotomy. This means that the animal needs to accelerate a lower mass, making it easier to obtain high velocities. Thus, sub-optimal limb posture might cancel out with the decrease in body mass. Given that we see a decrease in velocity, we predict that the relative recruitment of propulsive hindlimb muscles decreases following autotomy.

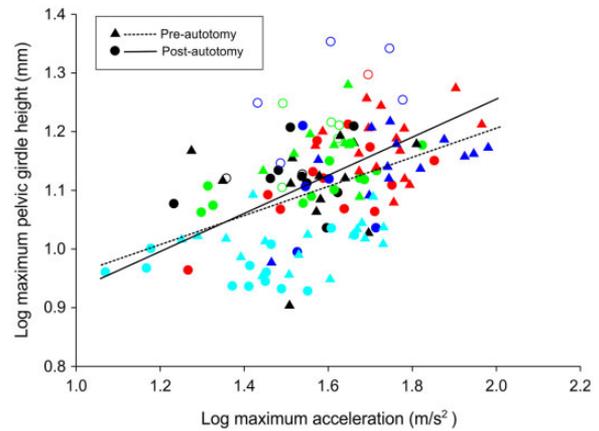
The number of post-autotomy trials recorded per day was insufficient to draw conclusions about the changes in velocity over time, but preliminary data indicate that velocity decreased in the trials recorded 2 h after autotomy but recovered 13 days after autotomy (Fig. 6). Recovery of maximum velocity over the 2-week period suggests that the geckos may be adjusting to the altered center of mass and the reduction in stability immediately following autotomy. Although it seems that geckos are able to regain effective striking without tails, the adjustments being



**Fig. 4** Average (A) starting height, (B) contact height, and (C) maximum height of the pectoral girdle, midpoint of the back, and pelvic girdle. Points show the average of the variable for each gecko, and each individual is color-coded to show variation. There was significant variation among individuals, although autotomy largely impacts the individuals similarly. Error bars represent SEM. Asterisks indicate a  $P < 0.05$ .

made to recover velocity are unknown. A future study with more trials per day over a longer period of time should explore the mechanism and degree to which velocity changes post-autotomy and over the course of regeneration.

Maximum acceleration was positively correlated with pelvic girdle height (Fig. 5), which is not surprising. The forces produced by the hindlimbs have vertical and horizontal components. Without the tail, the posterior mass of the lizard is reduced,

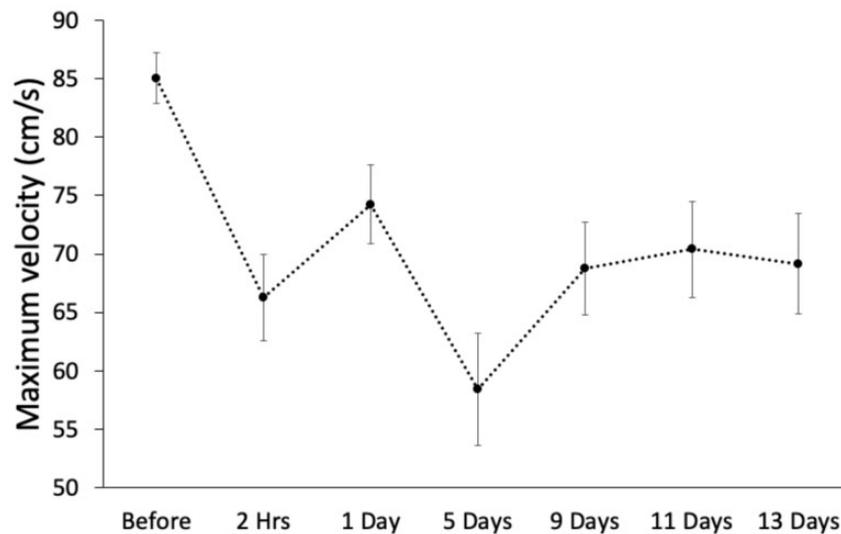


**Fig. 5** Linear regressions between maximum acceleration and maximum pelvic girdle height during a strike. Colors represent the individual geckos. Maximum pelvic girdle height is positively correlated with maximum acceleration. The slope of the regression before autotomy was 0.25,  $R^2 = 0.22$ ,  $P < 0.001$ . The slope of the regression after autotomy was 0.32,  $R^2 = 0.26$ ,  $P < 0.001$ .

which increases the relative force produced by the hindlimb muscles (if their activation remains the same). In post-autotomy trials, this occasionally caused the back legs to rise off the ground (Figs. 2 and 5), leading to an increased period of time required to return to resting position with the hindlimbs on the ground. Post-autotomy strikes exhibiting higher maximum acceleration resulted in the back legs elevating farther from the substrate. The decreased velocity and acceleration observed after autotomy may help the gecko avoid vertical displacement of the back legs and the potential fitness costs associated with the resulting instability and increased time to return to the resting position. A previous study on jumping in *Anolis carolinensis* found a high degree in individual variation to recover in-air stability after autotomy (Kuo et al. 2012). Our study suggests banded geckos may be similarly variable in their ability to modulate strike kinematics to optimize this pelvic girdle height/maximum acceleration trade-off.

### Comparisons with other lizards

There is an extensive body of literature on the feeding function of lizards (see Schwenk 2000; Bels et al. 2019; Montuelle and Kane 2019 for reviews). Lizards use either jaw or lingual prehension to capture prey. Thus, lizards (with some exceptions) must maneuver their jaws very close to the prey during the prey capture event. For rapid attacks on evasive prey, as in our study, the integration of locomotor and feeding events are critical (Higham 2007; Montuelle et al. 2009, 2012). Until recently, almost all of the work



**Fig. 6** Change in maximum velocity across pre- and post-autotomy trial with post-autotomy trials separated into days since tail removal. Error bars represent SEM. Trials conducted 2 h after autotomy had lower maximum velocity compared with trials conducted before autotomy, but velocity partially recovered over the 2 weeks following autotomy.

had focused on jaw mechanics or foraging strategies, rather than post-cranial movements leading up to prey capture. Montuelle et al. (2009) examined the integration of locomotion and feeding in *Gerrhosaurus major*. When the lizards capture evasive grasshoppers, the maximum strike velocity often reached approximately 1 m/s. Similarly, *Varanus* lizards often reach 1 m/s when striking at grasshoppers (Montuelle et al. 2012). At 85 cm/s pre-autotomy, the banded gecko has a comparable maximum strike velocity.

*Gerrhosaurus major* is a lizard capable of both jaw and lingual prehension, but utilizes jaw prehension to capture more elusive prey. Strikes using jaw prehension were also initiated at greater distances from the prey and at greater speeds (Montuelle et al. 2009). Banded geckos were only observed using jaw prehension in this study, consistent with previous studies suggesting that gekkonids almost exclusively use jaw prehension (Schwenk 2000), but the characteristics described in *G. major* jaw prehension-based feeding strikes appear to apply to the strikes observed in this study as well. Future testing of banded geckos with a second, less mobile prey type, will provide a more complete comparison. Some *G. major* individuals would also compress the vertebral axis into an “S” curve and rapidly extend during strikes (Montuelle et al. 2009), similar to the banded geckos (Fig. 1).

The variability of approaches to prey items found in banded geckos has been observed in other species. *Anolis carolinensis* display a similar locomotor plasticity, using both a “head-up capture” and a “jump

capture” to contact evasive prey (Montuelle et al. 2008). Four prey attack methods have been observed within anoles, including “jump-strikes,” which have been recorded in a variety of *Anolis* species (Moermond 1981). The strikes of banded geckos are also visually similar to those observed in neonate *Pogona vitticeps* (Bels et al. 2019). However, these species mainly use lingual prehension to capture prey, rather than the jaw prehension utilized by the banded geckos. How autotomy may impact prey capture in species that rely on lingual prehension should be studied in the future.

### Future directions

Although the reduction in performance and changes in kinematics following autotomy did not impact capture success in our laboratory experiments, these changes may play a significant role during strikes in nature. The significantly slower deceleration and longer period required to return to the resting position may also leave the gecko open to predator attacks or reduce the ability of the gecko to attempt a second strike immediately following an unsuccessful one. Banded geckos consume an array of prey types. Crickets are evasive, but other natural prey items may be more challenging. Flight-capable insects such as orthopterans and coleopterans made up over 32% of the gut contents of wild *C. variegatus* in one study (Parker and Pianka 1974), and strike dynamics are likely altered when geckos are attempting to capture prey out of the air. *Coleonyx variegatus* has also been observed to feed on highly venomous scorpions (Parker and Pianka 1974).

When capturing scorpions, geckos will shake their bodies to vigorously bash scorpions on the ground, presumably to remove the stinger (Whitford et al. manuscript under review). The removal of the tail could affect the gecko's ability to subdue this dangerous prey, resulting in a significant fitness impact for the gecko.

Given that the tail appears to be mainly for balance and stability, geckos may have a difficult time capturing prey in an uneven environment, such as the rocky deserts in which these geckos live. A study on wolf spiders found that prey capture ability was only affected in a high asperity substrate (Wrimm and Uetz 2008). *Coleonyx variegatus* geckos may similarly have difficulty capturing prey on an irregular surface. Future work could either provide a larger enclosure with a more natural substrate in a laboratory or could attempt to quantify strikes in nature before and after autotomy.

As noted above, the dynamics of prey capture rely on the rapid push-off from the hindlimbs. The loss of caudal mass and the anterior shift of the center of mass will alter the mechanics of the strike. Inverse dynamics, using both high-speed video and force plate recordings, would enable one to identify these changes. Additionally, neuromuscular recordings would reveal possible shifts in neural control during strikes, as is found during steady locomotion (Jagnandan and Higham 2018a).

Future studies should utilize autotomy to test how the tail is used in prey capture in other species of lizard. The integration of locomotion and feeding during prey capture has focused on the linkage between the jaws, neck, and forelimbs (Montuelle et al. 2009, 2012). However, our results highlight how the hindlimbs and tail, or lack thereof, can alter the strike performance and kinematics of lizards. Future research should examine the link between the use of the hindlimbs and the movement of the jaws in species that utilize a jump-strike hunting strategy and how this integration may be altered by tail autotomy.

Finally, eublepharid geckos are somewhat unique among lizards in that they have large and active tails. The tail of the geckos in our study accounted for up to 20% of the total body mass. Other carnivorous lizards also actively hunt prey, but many have relatively thin, rigid tails, such as the *Anolis* lizards mentioned above (Moermond 1981). *Anolis* tails are morphologically distinct from eublepharid tails and loss would likely impact strike dynamics differently. Examining the effect of autotomy on prey capture in species with relatively rigid tails could determine how the weight of the tail affects prey capture rather

than the movements of the tail. Similarly, arboreal lizards provide an opportunity to study the mechanics of hunting in complex 3D habitats. If tails are similarly important for braking and balance in arboreal species, the loss of the tail would incur a major fitness cost in species that hunt on narrow branches. Utilizing the diversity of lizards capable of tail autotomy can be the key to better understand tail function in terrestrial predation across a wide variety of ecological niches.

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## Data availability

Data for this project are available upon request.

## Conflict of interest

The author declares no conflicts of financial interest.

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