

COMMENTARY

Consequences of lost endings: caudal autotomy as a lens for focusing attention on tail function during locomotion

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ABSTRACT

Autotomy has evolved in many animal lineages as a means of predator escape, and involves the voluntary shedding of body parts. In vertebrates, caudal autotomy (or tail shedding) is the most common form, and it is particularly widespread in lizards. Here, we develop a framework for thinking about how tail loss can have fitness consequences, particularly through its impacts on locomotion. Caudal autotomy is fundamentally an alteration of morphology that affects an animal's mass and mass distribution. These morphological changes affect balance and stability, along with the performance of a range of locomotor activities, from running and climbing to jumping and swimming. These locomotor effects can impact on activities critical for survival and reproduction, including escaping predators, capturing prey and acquiring mates. In this Commentary, we first review work illustrating the (mostly) negative effects of tail loss on locomotor performance, and highlight what these consequences reveal about tail function during locomotion. We also identify important areas of future study, including the exploration of new behaviors (e.g. prey capture), increased use of biomechanical measurements and the incorporation of more field-based studies to continue to build our understanding of the tail, an ancestral and nearly ubiquitous feature of the vertebrate body plan.

KEY WORDS: Lizard, Running, Jumping, Performance

Introduction

Many of us learned in introductory biology about the fundamental anatomical features that characterize vertebrates and other chordates, including the tail, a post-anal extension of the body's axis and associated tissues (Kardong, 2009). As a fundamental feature of vertebrates, tails are also strikingly diverse. Consider the grossly asymmetrical caudal fin of the thresher shark as compared with its symmetrical counterpart in a great white, or the remarkable fan of the peacock relative to the long forked tail of the booted racket-tail hummingbird. Such anatomical diversity is matched by functional breadth. Tails are known to be used for mate attraction (Bischoff et al., 1985), mating (Shine et al., 1999), grasping (Garber and Rehg, 1999) and defense (Arbour, 2009), among many other specialized roles. However, tails are likely to have evolved in vertebrates as locomotory structures (Gans, 1989) and, as such, currently serve myriad functions in multiple environments, including aquatic propulsion (e.g. Feilich and Lauder, 2015; Flammang et al., 2011), balance in terrestrial and arboreal habitats (e.g. Larson and Stern, 2006; Walker et al., 1998) and in-air stability

and maneuverability during flight (e.g. Sachs, 2007; Schmieder et al., 2014).

Given this functionality, caudal autotomy, or the voluntary loss of parts of the tail, might strike some as a particularly extreme measure to employ when escaping a predator. However, extreme measures are often called for when life is on the line, and the prospect of losing an appendage becomes a little less problematic when that appendage can be regenerated. Among invertebrates, autotomized appendages vary widely and include limbs, antennae and feeding structures (Fleming et al., 2007). But in vertebrates, the tail is the appendage most commonly subject to this self-induced shedding. Although it is observed in a few mammals (e.g. Sumner and Collins, 1918) and amphibians (e.g. Wake and Dresner, 1967), caudal autotomy is most thoroughly studied in reptiles, and especially lizards (see Bateman and Fleming, 2009, for a recent review). Within lizards, interest has largely focused on understanding the potential costs of tail loss for the animal, which can include consequences for reproductive output, social status and energetics, in turn affecting an animal's fitness (Arnold, 1984; Maginnis, 2006). Loss of the tail can also impact on fitness by affecting the way an animal moves, and a rapidly growing body of work is exploring the impact(s) of caudal autotomy on locomotion and locomotor performance (see McElroy and Bergmann, 2013, for a recent review).

Although, from the animal's perspective, the loss of major portions of the tail may pose serious locomotor consequences, from the perspective of the functional morphologist, it opens opportunities to better understand the important roles that tails play during routine modes of locomotion. Indeed, one can think of caudal autotomy as presenting a natural experiment of sorts for studying how tails influence locomotor behavior. Like a physical or mathematical modeler who can remove or eliminate specific parts of a system to gain insight into what happens when they are gone, a functional morphologist studying autotomy can assess an animal's locomotion before and after tail loss, and make some inferences about the functional role of the tail when it is intact.

In this Commentary, we outline a framework for thinking about how tail loss affects locomotion (Fig. 1), and we review results from past studies to inform and support this framework. Finally, we also include a discussion of potential areas ripe for future research. Although a number of different vertebrate groups undergo caudal autotomy, including salamanders (Wake and Dresner, 1967), lizards (Bellairs and Bryant, 1985; Arnold, 1984), snakes (Cooper and Alfieri, 1993) and some rodents (McKee and Adler, 2002), the bulk of our discussion below will focus on lizards, which are by far the best-studied group in the context of how tail loss affects locomotion.

A framework for investigating caudal autotomy

In Fig. 1 we outline a framework, based on Arnold's morphology, performance, fitness paradigm (Arnold, 1983), and the expanded paradigm described by Garland and Losos (1994) that includes

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Glossary

Moment of inertia

A body's tendency or ability to resist rotation about an axis.

Ground reaction force

The force exerted by the ground against the body in reaction to the body's exertion of a force against the ground.

Inertial appendage

An appendage, like the tail, whose movements give rise to inertial forces that can be used to move or reorient the body.

behavior, for thinking about how tail loss ultimately can affect ecological functions with fitness consequences (such as predator evasion and prey capture) through its effects on locomotor biomechanics, behavior and performance. Here, we consider performance as a quantitative measure of how well an animal executes an ecologically relevant task that is vital for survival (Irschick and Higham, 2016). Thus, behavior and performance are inextricably linked (performance constrains behavior), and both are

constrained by biomechanics (Fig. 1). Caudal autotomy can be thought of simply as a change, albeit rapid and potentially quite radical, in morphology – an animal with an intact tail is transformed into an animal missing part or all of that tail. That change in morphology has physiological and biomechanical consequences, such as altering the position of the center of mass (CoM), decreasing available energy stores or modifying the way axial and limb muscles might be recruited (Fig. 1). Those physiological and biomechanical consequences can then alter performance (e.g. sprint speed) and locomotor behavior (e.g. running kinematics) that, in turn, can affect tasks relevant to fitness such as escaping predators or capturing prey (Fig. 1). Below, we review past literature to establish the validity of this framework, before proceeding to highlight important areas of future research.

Morphological, physiological and biomechanical consequences of tail loss

The two immediate consequences of losing part of the tail are the reduction in body mass and subsequent anteriorly directed shift in the animal's CoM (Figs 1 and 2). Lizard tails and bodies span a range of sizes and proportions, so autotomy events can have a variety of impacts on body mass. For example, an animal with a long slender tail that autotomizes just the tip is likely to experience a negligible change in body mass as compared with animals with more robust tails, which can account for close to 25% of body mass (Higham and Russell, 2010; Jagnandan et al., 2014). Similarly, subsequent shifts in the position of the CoM can be negligible or up to 15–20% of snout–vent length, depending on the amount of tail lost and the relative length and mass of the tail in relation to the body (Fig. 2). In some lizards, the tail is also an important site for storing lipids, so that in addition to losing mass and having their CoM position shift, animals may also be losing critical energy stores when parts of a tail are lost (e.g. Dial and Fitzpatrick, 1981; Fleming et al., 2009).

Further, in addition to causing a rapid change in body mass, caudal autotomy can lead to reduced frictional resistance in animals whose tails drag against the ground (Snyder, 1952). And in species for which the tail serves as an inertial appendage (see Glossary) (Jusufo et al.,

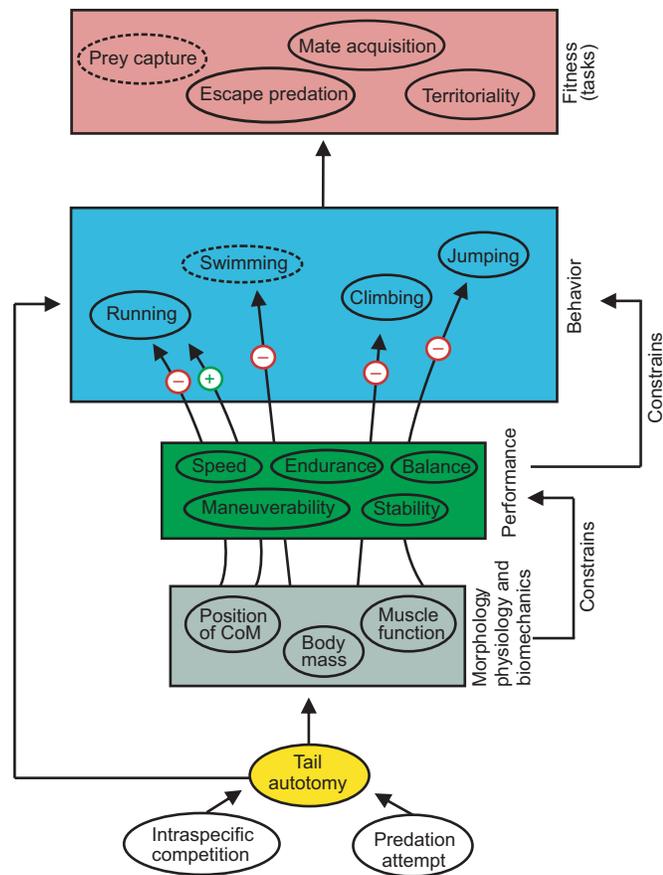


Fig. 1. A framework for thinking about the ways in which autotomy can affect organismal fitness. Autotomy affects morphology, physiology and biomechanics by altering several key traits, and these in turn will alter behavioral outcomes via changes in performance. Lower level traits (e.g. morphology) will constrain higher level traits (e.g. performance), and performance will constrain behavior. The ultimate result of autotomy is a change in fitness, although more work is needed across diverse species to determine whether this is widespread. Finally, tail autotomy can have a direct impact on behavior (arrow on left), for example, by causing a shift from arboreal to terrestrial locomotion. Any terms surrounded by a dashed ellipse have received little to no attention and should be a focus of future work. Red minus symbols indicate a negative effect of caudal autotomy on a particular behavior; green plus symbols indicate positive effects.

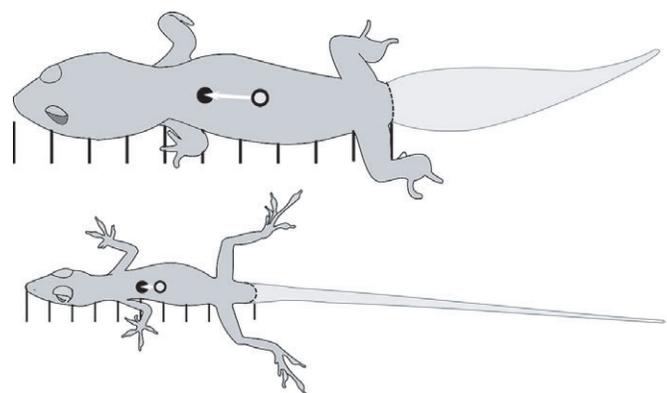


Fig. 2. Tail loss affects the position of the center of mass. Images of a leopard gecko (top) and green anole (bottom) showing how tail loss affects the position of the center of mass (CoM). The dashed line denotes where the tail would be autotomized, and the arrow denotes the subsequent expected anterior shift in the CoM. Lizards are drawn at different scales and the vertical black lines represent 10% snout–vent length increments. Note that both tail mass (in the case of the gecko) and tail length (in the case of the anole) are important factors in determining the degree to which tail loss will affect CoM position. Data for the leopard gecko are based on Jagnandan et al. (2014) and those for the anole are based on Hsieh (2016).

2010), the decreased moment of inertia (see Glossary) associated with autotomy events is also likely to have locomotor effects.

Changes in overall mass and mass distribution that result from full or partial tail loss are also likely to lead to changes in locomotor mechanics. Very few studies have examined locomotor kinetics following autotomy; however, a recent study of the leopard gecko, *Eublepharis macularius*, demonstrated that these animals adopted a more sprawled hindlimb posture following tail loss, along with reduced peak hindlimb vertical ground reaction forces (see Glossary), corrected for body size (Jagnandan et al., 2014). Similarly, recent work on green anoles, *Anolis carolinensis*, also demonstrated a more crouched hindlimb posture during perch running after tail autotomy (Hsieh, 2016). As more studies begin to measure ground reaction forces and detailed kinematics of running lizards before and after tail loss, we will be better positioned to develop predictive frameworks for understanding how autotomy influences locomotor behavior and performance. Until then, we can rely on a wide range of studies from the past 50 years as well as several recent and thorough reviews (Bateman and Fleming, 2009; Higham et al., 2013b; McElroy and Bergmann, 2013) to seek patterns to help us understand the impacts of tail loss on different locomotor modes, as discussed below.

Effects of tail loss on locomotor behavior and performance

It might seem intuitive that losing a body part will negatively affect the ability of an animal to perform a behavior, especially when that behavior relies on or involves the use of the lost body part. Below, we review and synthesize results from previous work examining how autotomy can affect different locomotor behaviors. In addition to the growing body of work examining the varied effects of caudal autotomy on running, recent work is also illuminating the importance of the tail during more diverse activities, including climbing (e.g. Chapple and Swain, 2002), jumping (e.g. Gillis et al., 2009) and swimming (e.g. Marvin, 2010). We discuss the consequences of autotomy on each of these locomotor modes, although not all aspects of performance, behavior and fitness, as highlighted in Fig. 1, have been investigated for each. We begin by examining running, the most well-studied locomotor behavior to date.

Running

Caudal autotomy often impairs running

Running quickly is often critical for escaping from predators, and given that tails are known to be important for balance and maneuvering in terrestrial locomotion (Walker et al., 1998), it seems reasonable to expect that caudal autotomy will affect aspects of running ability. However, because the tail is not directly involved in propulsion during lizard running, the extent to which autotomy might affect speed is less obvious. Given the relative ease of measuring speed, we are in the fortunate position of having had many species of lizard examined in this context. A recent review of the literature for lizards reveals that locomotor performance decreased as a result of caudal autotomy in 65% of studies, whereas no effect (26%) or even an increase in performance (9%) was observed in the remaining studies (McElroy and Bergmann, 2013). Such disparity in outcomes may reflect methodological differences among studies as well as clade-specific tendencies within lizards (with respect to how autotomy affects performance, e.g. McElroy and Bergmann, 2013).

Nevertheless, given that roughly two out of three studies reveal that tail loss negatively impacts on locomotor performance, McElroy and Bergmann (2013) suggest it is reasonable to conclude that tails are important for running speed in lizards. First, autotomy studies

have shown that tail loss leads to decreases in stride length, suggesting the importance of the tail for maintaining long strides (Hamley, 1990; Martin and Avery, 1998). Second, removal of the tail leads to the CoM moving anteriorly, farther from the hindlimbs (Fig. 2), and so intact tails help to position the CoM closer to the hindlimbs where force is generated against the ground (Ballinger et al., 1979). Third, lizards adopt a more sprawled posture during running after autotomy (Hsieh, 2016; Jagnandan et al., 2014), suggesting that tails likely serve to improve balance and stability.

Compensating for the loss of the tail

It is important to consider that a full third of studies find that autotomy either has no effect on speed or actually increases it (McElroy and Bergmann, 2013). In such cases, is the tail simply not important for running fast? Maybe, but there might be more parsimonious explanations. As mentioned above, several authors have noted that stride length decreases following autotomy, which often results in a decrease in sprint performance (Anderson et al., 2012; Martin and Avery, 1998). But locomotor speed depends on both stride length and stride frequency (Alexander, 2003), which means that stride frequency could be modulated to compensate for, or even overcome, decreases in stride length. Movements of the hind limbs are mechanically coupled to movements of the tail, such that stride frequency and tail oscillation frequency match (Hamley, 1990). When the tail is lost, this coupling is lost, which permits increases in stride frequency (Hamley, 1990; Martin and Avery, 1998). Indeed, water dragons, *Physignathus lesueurii*, compensate for the reduced stride length associated with tail loss by increasing stride frequency to maintain high speeds (Hamley, 1990).

Why don't all lizards compensate and maintain performance in this way? One possibility is that the loss of the tail reduces stability (Brown et al., 1995), leading lizards to deliberately reduce speed (Fig. 1) rather than risking balance and control. Another possibility is that tail fractures that occur near the base might injure the m. caudofemoralis (Barbadillo et al., 1995) or reduce its efficiency (Arnold, 1994; Russell et al., 2001). Either outcome for such an important femoral retractor would be likely to limit stride frequency and prevent compensation accordingly. A third possibility is that stride frequency in intact animals during sprinting is already near a level that reflects the mechanical and energetic limit of the muscles, i.e. there is no 'room for improvement'. Finally, a fourth possibility relates to potential energetic constraints underlying an animal's inability to maintain speed following autotomy. Work on locomotor energetics in the Cape dwarf gecko, *Lygodactylus capensis*, revealed reduced stamina and speed after tail loss, perhaps due to metabolic constraints associated with the loss of fatty fuel sources after autotomy (Fleming et al., 2009). A paucity of studies combine measurements of locomotor performance with detailed analyses of limb kinematics and mechanics or whole-animal energetics, so the mechanisms underlying a change in performance are often not known (but see Jagnandan et al., 2014, for recent work integrating kinematics and mechanics before and after autotomy).

Running and maneuverability

During running, maneuverability is likely to be critical for the success of activities like escaping predators and chasing prey. The effects of autotomy on maneuvers such as rapid turns, however, have not been well explored. There are reasons to believe that tail loss could exert opposing effects on turning performance. For example, any loss in stability that occurs after tail loss, as the CoM is shifted further from where the hindlimbs are generating force, is likely to make it harder for an animal to control rapid, sharp turns.

Similarly, as inertial appendages, tails can be used to counter destabilizations during rapid maneuvers, and this ability would be compromised after autotomy. However, although controlling rapid turns is likely to be more difficult after tail loss, the physical ease of turning itself might be improved. An animal's rotational inertia, or resistance to rotation, is a function of how its mass is distributed in relation to the location of the rotational axis of interest. Tails can add mass far from the turning body, thus increasing the body's rotational inertia and making it more difficult to turn (Carrier et al., 2001; Walter and Carrier, 2002). But tails tend to be less rigid and more mobile than those modeled in the aforementioned studies, and hence the question of whether reductions in tail length might improve turning performance as a result of reduced rotational inertia in lizards remains to be determined.

Climbing

Arboreal lizards routinely encounter inclined and vertical surfaces, and must be able to navigate such surfaces quickly to capture prey or evade predators. The importance of the tail for climbing performance appears to vary among lizard species. For example, autotomy has no effect on climbing speed in the metallic skink, *Niveoscincus metallicus* (Chapple and Swain, 2002), or the flat-tailed house gecko, *Cosymbotus platyurus* (Jusufi et al., 2008), but reduces climbing speed in the Cape dwarf gecko (Medger et al., 2008) and the wall lizard, *Podarcis muralis* (Brown et al., 1995). Speed aside, two of these studies reveal a critical function for the tail during climbing in geckos; namely, preventing falling by increasing the animal's stability (Medger et al., 2008; Jusufi et al., 2008). Both studies found that after tail loss, animals were more prone to pitching backwards and falling off the climbing surface. High-speed video and force platform analyses of animals climbing with intact tails (Jusufi et al., 2008) pointed to the importance of the tail interacting with the climbing surface to overcome destabilizations and help prevent falls during climbing. Moreover, induced autotomy experiments and analytical modeling crystallized that the lizard's tail played another critical function after the animal had fallen; namely, to coordinate righting behavior before landing (Jusufi et al., 2008, 2011).

Jumping

Like climbing, jumping is another common form of locomotion among arboreal lizards seeking to capture prey or escape predators (Irschick and Losos, 1998; Losos and Irschick, 1996). Work focusing on whether autotomy affects jumping shows that jump distance is not compromised by tail loss (Fleming and Bateman, 2012; Gillis et al., 2009). However, tails are likely to be important for stability to control landing, as they can be used as inertial appendages to control body position in mid-air (Jusufi et al., 2010) or can interact with the substrate during takeoff to prevent over-rotation after the animal leaves the ground (Gillis et al., 2009). Indeed, landing coordination has now been shown to be compromised in autotomized individuals in multiple species: jumping green anoles, jumping Cape dwarf geckos and falling flat-tailed house geckos (Fleming and Bateman, 2012; Gillis et al., 2009, 2013; Jusufi et al., 2008). In addition, red-headed Agama lizards, *Agama agama*, swing their tails to adjust body pitch when vaulting over obstacles, and models of tailless lizards indicate the importance of this tail swinging for overcoming perturbations during these running jumps (Libby et al., 2012).

Swimming

Although most work on caudal autotomy in vertebrates has focused on lizards, salamanders are also known to undergo autotomy of the

tail (Maiorana, 1977; Wake and Dresner, 1967), although only a few studies have explored its effects on locomotion. Work on swimming in plethodontid salamanders (genus *Desmognathus*) demonstrates that burst speeds are reduced ~40–50% following loss of 2/3 of the tail in both terrestrial and semi-aquatic species (Marvin, 2010). Additional experiments indicated that more than 15% of the tail needed to be lost before decreases in maximum swimming performance were observed (Marvin, 2013). Work on swimming in a lizard, the water skink, *Sphenomorphus quoyii*, also revealed a decrease in speed of ~45% following tail removal (Daniels, 1985).

Further impacts on behavior and performance

Locomotion is central to many activities that determine whether a lizard lives or dies, mates successfully, or leaves few or no offspring. As described above, autotomy can have severe consequences for diverse locomotor activities, from running and jumping to climbing and swimming (Fig. 1). Although little field work exists to actually tie tail loss to specific fitness consequences, lab-based studies have routinely drawn this connection. Most lizards rely on speed to escape predators or capture prey, and given that sprint speed (McElroy and Bergmann, 2013), climbing speed (Brown et al., 1995) and swimming speed (Daniels, 1985) are often reduced significantly after tail loss, it is easy to conclude that such locomotor handicaps will have effects on an animal's ability to capture prey, and escape being fed upon, post-autotomy. Similarly, for arboreal lizards, uncoordinated landing or compromised balance and stability on fine branches may hinder prey capture or even lead to falling out of the tree onto the ground, increasing exposure to predators.

Tails are also well known as sites of lipid storage (Dial and Fitzpatrick, 1981) and, as such, effectively represent fuel depots that are lost after autotomy. Although some lizards recuperate some of this energy by returning to the site of autotomy and eating their own tail (Clark, 1971), many lizards lose significant energy resources following tail loss. Moreover, any energy that subsequently has to be put into tail regeneration is unavailable for other activities, including growth, locomotion, feeding and mating, all of which can have a significant impact on an animal's fitness (Bateman and Fleming, 2009).

Future research

Although the impact of caudal autotomy on the locomotion of terrestrial vertebrates, especially lizards, has received considerable attention over the past few decades, many important questions remain open. Here, we outline potential areas of future research, most stemming from recent and intriguing forays into these areas.

Regeneration

Given that most lizards are capable of eventually regenerating parts of a lost tail, it is possible that some aspects of tail function and thus locomotor performance can be regained, although this may not be as straightforward as it sounds. The skeleton of the original tail is composed of a series of bony vertebrae, but the regenerate is an unsegmented, hollow cartilaginous cone (Gilbert et al., 2014). In addition to the altered skeletal arrangement, the neuromuscular composition differs dramatically between the original and the regenerate (Bellairs and Bryant, 1985; Fisher et al., 2012; Gilbert et al., 2014; Higham et al., 2013a; McLean and Vickaryous, 2011). Muscle bundles, for example, are arranged in an asymmetric way in the regenerated tail, and the number of bundles varies among locations along the length of the tail (Gilbert et al., 2014). Contraction kinetics, isometric force, work, power output and the oscillation frequency at which maximum power is generated are all

lower in the original tail muscle compared with the muscle in the regenerate, leading to a more powerful but more fatigable regenerate (Higham et al., 2013a). The many differences between the original tail and the regenerate likely translate into operational differences during locomotion (Higham et al., 2013a); however, surprisingly little is known about regenerate function.

The question of whether the negative consequences of caudal autotomy for locomotion are temporary has been addressed in a small number of studies (Chapple and Swain, 2002; Downes and Shine, 2001; Jagnandan et al., 2014), but results have varied. For example, in the garden skink, *Lampropholis guichenoti*, running performance was regained 6 weeks following autotomy (Downes and Shine, 2001). In contrast, sprint performance of male metallic skinks was never restored, even after regrowth of 45–50% of the original tail length (Chapple and Swain, 2002).

Given that previous work has shown that regenerates are capable of generating higher power output and force with tail muscles, and can operate at higher frequencies (Higham et al., 2013a), it is possible that lizards could actually run faster following regeneration. However, the change in structure among tail muscles in regenerates might convey a lack of control and therefore decreased locomotor stability. Teasing apart the impacts of structural and physiological changes in regenerated tails, in the context of whether and when performance is regained, should be an interesting area of future investigation.

Prey capture and maneuvering

Despite recent studies on aerial righting (Jusufi et al., 2008), slip recovery (Jusufi et al., 2008) and jumping (Gillis et al., 2009), the majority of the work on caudal autotomy and lizard locomotion has focused on running (McElroy and Bergmann, 2013). We suggest continued work on how autotomy affects performance of other locomotor modes germane to lizards, including swimming, climbing and jumping. In addition, we propose two additional areas, often related to running, that are understudied in the context of caudal autotomy but are likely to be affected by tail loss and are important for animal survival. The first is capturing prey, a task very important for fitness. The success of rapid predatory attacks that utilize the locomotor system could be significantly affected by tail loss and regeneration (Fig. 1). Successful prey capture requires both accuracy and high acceleration, and tail loss could impede both, hence reducing the ability to capture prey.

A second area in need of more attention is maneuvering performance. The execution of rapid turns, for example, is important as animals navigate complex environments and escape from potential predators or attempt to capture evading prey. As noted above, understanding how tail length, and thus caudal autotomy, might affect turning maneuvers has been touched on in the literature (Carrier et al., 2001; Jusufi et al., 2010; Walter and Carrier, 2002). This topic is particularly intriguing because although longer tails can help in turning the body (Jusufi et al., 2010), a shorter tail (i.e. post-autotomy) could decrease rotational inertia, making it easier to turn when running (Walter and Carrier, 2002). More focused examinations of how autotomy affects maneuvers like running turns, and whether and how regeneration influences this should be undertaken.

Neuromuscular control

Muscles actuate movements and can act as brakes and stabilizers. Numerous studies have examined these roles during locomotion in a variety of terrestrial vertebrates and across a range of surfaces (Gillis et al., 2005; Higham and Jayne, 2004; McGowan et al., 2007;

Roberts et al., 1997). How neuromuscular control of the limbs and axial system is modulated, if at all, in response to sudden shifts in the location of the CoM, and changes in body mass, is a rich area for future work and will provide insight into the functional versatility of musculoskeletal systems and their control (Gillis and Biewener, 2003). Understanding whether animals modulate motor output to locomotor muscles could also inform questions about the reduced performance that often accompanies caudal autotomy (Fig. 1). With the almost instantaneous loss of one-quarter of body mass, are limb and/or axial muscles being recruited differently following autotomy? Are these differences realized immediately or do they develop over time? Finally, are motor patterns restored following tail regeneration, or is there a fundamental coupling of limb and tail muscle function, the control of which is forever lost when the original tail is sundered? Given how readily animals modulate the neuromuscular control of locomotion depending on external conditions (e.g. load or environment; Gillis and Blob, 2001), and given that postural shifts are observed after autotomy (Jagnandan et al., 2014), we hypothesize that lizards, especially those with relatively large tails, quickly alter aspects of motor output to important muscles to help account for the changes in mass and CoM position associated with tail loss. Using electromyography to quantify limb and axial muscle activation patterns before and after autotomy would illuminate any shifts in motor control that result from losing part or all of the tail.

Biomechanics

Most studies of the effects of caudal autotomy on locomotion have focused on overall performance, often measured as speed (reviewed in McElroy and Bergmann, 2013). We encourage future work to continue to integrate more detailed measurements of locomotor kinematics and kinetics before and after tail loss. Once we begin to understand how autotomy is affecting foot–ground interactions, force development and movement patterns of the limbs and body, we will be in a better position to explain why locomotor performance is affected in specific ways in particular species, and may also begin to pick up on trends that are clade specific, or dependent on the size, shape and usage patterns of the intact tail.

Ecological context

The ecological context of tail autotomy must be considered when addressing the post-autotomic behavior of both the tail and lizard. Tails can serve different roles depending on the environment; thus, lizards that live in arboreal environments, for example, are likely to experience different consequences following autotomy than lizards that occupy a relatively flat desert habitat. As we continue to study and identify particular consequences of autotomy, we must also remain aware that these will be intertwined with ecology. Just as an animal's habitat is likely to influence the particular locomotor costs of autotomy, the loss of the tail itself might also affect the ways in which an animal uses its habitat (Fig. 1). For example, if climbing or balance on fine branches is severely compromised following tail loss in an arboreal lizard, the animal may move for a time out of the trees and onto the forest floor, switching behaviors from climbing to running (Fig. 1). Indeed, a recent study of the arboreal green anole showed that running kinematics were affected by a combination of perch diameter and autotomy (Hsieh, 2016). Tail regeneration may restore locomotor kinematics and ability, leading to a restoration of the original patterns of habitat use, but more fieldwork is required to understand the effects of autotomy on locomotion and other behaviors in a more natural context. Exploring ecological patterns

such as that mentioned above is likely to provide a rich source of information in future studies.

Conclusions

Ablation, as a tool, is a classic experimental approach to studying structure–function relationships – remove a structure and explore the consequences to learn something about the role of that structure. Caudal autotomy represents a naturally occurring form of gross, structural ablation, and affords us the opportunity to greatly enhance our understanding of a fundamental component of vertebrate anatomy – the tail. Tail loss results in reduced mass and a displaced CoM, but it is also clear that it represents the loss of an important functional appendage. Its importance for locomotion is convincingly demonstrated by ample studies of reduced performance, largely measured during running to date, but also during more diverse locomotor modes such as climbing, swimming and jumping. How tails are actually used during these activities and others to affect performance requires more attention, but many studies of autotomy have provided good insight into species and behaviors that should be explored in more detail.

Although most autotomy studies in vertebrates will be limited to lizards, they are an excellent model group because they are ecologically diverse and use the tail in many ways. We look forward to future autotomy studies exploring new behaviors (e.g. prey capture), using biomechanical approaches and taking advantage of field-based opportunities to continue to build our understanding of the integrative biology of the tail.

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References

- Alexander, R. M. (2003). *Principles of Animal Locomotion*. Princeton: Princeton University Press.
- Anderson, M. L., Cavalieri, C. N., Rodriguez-Romero, F. and Fox, S. F. (2012). The differential effect of tail autotomy on sprint performance between the sexes in the lizard *Uta stansburiana*. *J. Herpetol.* **46**, 648–652.
- Arbour, V. M. (2009). Estimating impact forces of tail club strikes by Ankylosaurid dinosaurs. *PLoS ONE* **4**, e6738.
- Arnold, S. J. (1983). Morphology, performance and fitness. *Am. Zool.* **23**, 347–361.
- Arnold, E. N. (1984). Evolutionary aspects of tail shedding in lizards and their relatives. *J. Nat. Hist.* **18**, 127–169.
- Arnold, E. N. (1994). Investigating the evolutionary effects of one feature on another: does muscle spread suppress caudal autotomy in lizards? *J. Zool.* **232**, 505–523.
- Ballinger, R. E., Nietfeldt, J. W. and Krupa, J. J. (1979). An experimental analysis of the role of the tail in attaining high running speed in *Cnemidophorus sexlineatus* (Reptilia: Squamata: Lacertilia). *Herpetologica* **35**, 114–116.
- Barbadillo, L. J., Bauwens, D., Barahona, F. and Sanchez-Herráiz, M. J. (1995). Sexual differences in caudal morphology and its relation to tail autotomy in Lacertid lizards. *J. Zool.* **236**, 83–93.
- Bateman, P. W. and Fleming, P. A. (2009). To cut a long tail short: A review of lizard caudal autotomy studies carried out over the last 20 years. *J. Zool.* **277**, 1–14.
- Bellairs, A. and Bryant, S. V. (1985). Autotomy and regeneration in reptiles. In *Biology of the Reptilia. Development* **15**, 301–410.
- Bischoff, R. J., Gould, J. L. and Rubenstein, D. (1985). Tail size and female choice in the guppy (*Poecilia reticulata*). *Behav. Ecol. Sociobiol.* **17**, 253–255.
- Brown, R. M., Taylor, D. H. and Gist, D. H. (1995). Effect of caudal autotomy on locomotor performance of wall lizards (*Podarcis muralis*). *J. Herpetol.* **29**, 98–105.
- Carrier, D. R., Lee, D. V., Walter, R. M. and Deban, S. M. (2001). Influence of increased rotational inertia on the turning performance of humans. *J. Exp. Biol.* **204**, 3927–3934.
- Chapple, D. G. and Swain, R. (2002). Effect of caudal autotomy on locomotor performance in a viviparous skink, *Niveoscincus metallicus*. *Funct. Ecol.* **16**, 817–825.
- Clark, D. R. (1971). The strategy of tail-autotomy in the ground skink, *Lygosoma laterale*. *J. Exp. Zool.* **176**, 295–302.
- Cooper, W. E. and Alfieri, K. J. (1993). Caudal autotomy in the eastern garter snake, *Thamnophis sirtalis*. *Amphibia-Reptilia* **14**, 86–89.
- Daniels, C. B. (1985). The effect of tail autotomy on the exercise capacity of the water skink, *Sphenomorphus quoyii*. *Copeia* **1985**, 1074–1077.
- Dial, B. E. and Fitzpatrick, L. C. (1981). The energetic costs of tail autotomy to reproduction in the lizard *Coleonyx brevis* (Sauria: Gekkonidae). *Oecologia* **51**, 310–317.
- Downes, S. and Shine, R. (2001). Why does tail loss increase a lizard's later vulnerability to snake predators? *Ecology* **82**, 1293–1303.
- Feilich, K. L. and Lauder, G. V. (2015). Passive mechanical models of fish caudal fins: effects of shape and stiffness on self-propulsion. *Bioinspir. Biomim.* **10**, 036002.
- Fisher, R. E., Geiger, L. A., Stroik, L. K., Hutchins, E. D., George, R. M., Denardo, D. F., Kusumi, K., Rawls, J. A. and Wilson-Rawls, J. (2012). A histological comparison of the original and regenerated tail in the green anole, *Anolis carolinensis*. *Anat. Rec.* **295**, 1609–1619.
- Flammang, B. E., Lauder, G. V., Troolin, D. R. and Strand, T. (2011). Volumetric imaging of shark tail hydrodynamics reveals a three-dimensional dual-ring vortex wake structure. *Proc. R. Soc. B Biol. Sci.* **278**, 3670–3678.
- Fleming, P. A. and Bateman, P. W. (2012). Autotomy, tail regeneration and jumping ability in Cape dwarf geckos (*Lygodactylus capensis*) (Gekkonidae). *Afr. Zool.* **47**, 55–59.
- Fleming, P. A., Muller, D. and Bateman, P. W. (2007). Leave it all behind: a taxonomic perspective of autotomy in invertebrates. *Biol. Rev.* **82**, 481–510.
- Fleming, P. A., Verburgt, L., Scantlebury, M., Medger, K. and Bateman, P. W. (2009). Jettisoning ballast or fuel? Caudal autotomy and locomotor energetics of the Cape dwarf gecko *Lygodactylus capensis* (Gekkonidae). *Physiol. Biochem. Zool.* **82**, 756–765.
- Gans, C. (1989). Stages in the origin of vertebrates: analysis by means of scenarios. *Biol. Rev.* **64**, 221–268.
- Garber, P. A. and Rehg, J. A. (1999). The ecological role of the prehensile tail in white-faced capuchins (*Cebus capucinus*). *Am. J. Phys. Anthropol.* **110**, 325–339.
- Garland, T., Jr. and Losos, J. B. (1994). Ecological morphology of locomotor performance in squamate reptiles. In *Ecological Morphology: Integrative Organismal Biology* (ed. P. C. Wainwright and S. M. Reilly), pp. 240–302. Chicago: University of Chicago Press.
- Gilbert, E. A. B., Payne, S. L. and Vickaryous, M. K. (2014). The anatomy and histology of caudal autotomy and regeneration in lizards. *Physiol. Biochem. Zool.* **86**, 631–644.
- Gillis, G. B. and Biewener, A. A. (2003). The importance of functional plasticity in the design and control of the vertebrate musculoskeletal system. In *Vertebrate Biomechanics and Evolution* (ed. V. L. Bels, J.-P. Gasc and A. Casinos), pp. 57–72. Oxford: BIOS Scientific Publishers.
- Gillis, G. B. and Blob, R. W. (2001). How muscles accommodate movement in different physical environments: aquatic vs. terrestrial locomotion in vertebrates. *Comp. Biochem. Physiol. A Mol. Integr. Physiol.* **131**, 61–75.
- Gillis, G. B., Flynn, J. P., McGuigan, P. and Biewener, A. A. (2005). Patterns of strain and activation in the thigh muscles of goats across gaits during level locomotion. *J. Exp. Biol.* **208**, 4599–4611.
- Gillis, G. B., Bonvini, L. A. and Irschick, D. J. (2009). Losing stability: tail loss and jumping in the arboreal lizard *Anolis carolinensis*. *J. Exp. Biol.* **212**, 604–609.
- Gillis, G. B., Kuo, C.-Y. and Irschick, D. (2013). The impact of tail loss on stability during jumping in green anoles (*Anolis carolinensis*). *Physiol. Biochem. Zool.* **86**, 680–689.
- Hamley, T. L. (1990). Functions of the tail in bipedal locomotion of lizards, dinosaurs and pterosaurs. *Mem. Queensl. Mus.* **28**, 153–158.
- Higham, T. E. and Jayne, B. C. (2004). *In vivo* muscle activity in the hindlimb of the arboreal lizard, *Chamaeleo calytratus*: general patterns and the effects of incline. *J. Exp. Biol.* **207**, 249–261.
- Higham, T. E. and Russell, A. P. (2010). Flip, flop and fly: modulated motor control and highly variable movement patterns of autotomized gecko tails. *Biol. Lett.* **6**, 70–73.
- Higham, T. E., Lipsett, K. R., Syme, D. A. and Russell, A. P. (2013a). Controlled chaos: three-dimensional kinematics, fiber histochemistry, and muscle contractile dynamics of autotomized lizard tails. *Physiol. Biochem. Zool.* **86**, 611–630.
- Higham, T. E., Russell, A. P. and Zani, P. A. (2013b). Integrative biology of tail autotomy in lizards. *Physiol. Biochem. Zool.* **86**, 603–610.
- Hsieh, S.-T. T. (2016). Tail loss and narrow surfaces decrease locomotor stability in the arboreal green anole lizard (*Anolis carolinensis*). *J. Exp. Biol.* **219**, 364–373.
- Irschick, D. J. and Higham, T. E. (2016). *Animal Athletes: An Ecological and Evolutionary Approach*. Oxford: Oxford University Press.
- Irschick, D. J. and Losos, J. B. (1998). A comparative analysis of the ecological significance of maximal locomotor performance in Caribbean *Anolis* lizards. *Evolution* **52**, 219–226.
- Jagnandan, K., Russell, A. P. and Higham, T. E. (2014). Tail autotomy and subsequent regeneration alter the mechanics of locomotion in lizards. *J. Exp. Biol.* **217**, 3891–3897.
- Jusufi, A., Goldman, D. I., Revzen, S. and Full, R. J. (2008). Active tails enhance arboreal acrobatics in geckos. *Proc. Natl. Acad. Sci. USA* **105**, 4215–4219.
- Jusufi, A., Kawano, D. T., Libby, T. and Full, R. J. (2010). Righting and turning in mid-air using appendage inertia: reptile tails, analytical models and bio-inspired robots. *Bioinspir. Biomim.* **5**, 045001.

- Jusufi, A., Zeng, Y., Full, R. J. and Dudley, R.** (2011). Aerial righting reflexes in flightless animals. *Integr. Comp. Biol.* **51**, 937-943.
- Kardong, K. V.** (2009). *Vertebrates: Comparative Anatomy, Function, Evolution*. 5th edn. New York: McGraw Hill.
- Larson, S. G. and Stern, J. T.** (2006). Maintenance of above-branch balance during primate arboreal quadrupedalism: coordinated use of forearm rotators and tail motion. *Am. J. Phys. Anthropol.* **129**, 71-81.
- Libby, T., Moore, T. Y., Chang-Siu, E., Li, D., Cohen, D. J., Jusufi, A. and Full, R. J.** (2012). Tail-assisted pitch control in lizards, robots and dinosaurs. *Nature* **481**, 181-184.
- Losos, J. B. and Irschick, D. J.** (1996). The effect of perch diameter on escape behaviour of *Anolis* lizards: laboratory predictions and field tests. *Anim. Behav.* **51**, 593-602.
- Maginnis, T. L.** (2006). The costs of autotomy and regeneration in animals: a review and framework for future research. *Behav. Ecol.* **17**, 857-872.
- Maiorana, V. C.** (1977). Tail autotomy, functional conflicts and their resolution by a salamander. *Nature* **265**, 533-535.
- Martin, J. and Avery, R. A.** (1998). Effects of tail loss on the movement patterns of the lizard, *Psammotromus algirus*. *Funct. Ecol.* **12**, 794-802.
- Marvin, G. A.** (2010). Effect of caudal autotomy on aquatic and terrestrial locomotor performance in two Desmognathine salamander species. *Copeia* **2010**, 468-474.
- Marvin, G. A.** (2013). Critical tail autotomy for reduction of maximal swimming performance in a Plethodontid salamander (*Desmognathus quadramaculatus*). *J. Herpetol.* **47**, 174-178.
- McElroy, E. J. and Bergmann, P. J.** (2013). Tail autotomy, tail size, and locomotor performance in lizards. *Physiol. Biochem. Zool.* **86**, 669-679.
- McGowan, C. P., Baudinette, R. V. and Biewener, A. A.** (2007). Modulation of proximal muscle function during level versus incline hopping in tammar wallabies (*Macropus eugenii*). *J. Exp. Biol.* **210**, 1255-1265.
- McKee, R. C. and Adler, G. H.** (2002). Tail autotomy in the Central American spiny rat, *Proechimys semispinosus*. *Stud. Neotrop. Fauna Environ.* **37**, 181-185.
- McLean, K. E. and Vickaryous, M. K.** (2011). A novel amniote model of epimorphic regeneration: the leopard gecko, *Eublepharis macularius*. *BMC Dev. Biol.* **11**, 50.
- Medger, K., Verburgt, L. and Bateman, P. W.** (2008). The influence of tail autotomy on the escape response of the Cape Dwarf Gecko, *Lygodactylus capensis*. *Ethology* **114**, 42-52.
- Roberts, T. J., Marsh, R. L., Weyland, P. G. and Taylor, C. R.** (1997). Muscular force in running turkeys: the economy of minimizing work. *Science* **275**, 1113-1115.
- Russell, A. P., Bergmann, P. J. and Barbadillo, L. J.** (2001). Maximal caudal autotomy in *Podarcis hispanica* (Lacertidae): the caudofemoralis muscle is not sundered. *Copeia* **2001**, 154-163.
- Sachs, G.** (2007). Tail effects on yaw stability in birds. *J. Theor. Biol.* **249**, 464-472.
- Schmieder, D. A., Zsebók, S. and Siemers, B. M.** (2014). The tail plays a major role in the differing manoeuvrability of two sibling species of mouse-eared bats (*Myotis myotis* and *Myotis blythii*). *Can. J. Zool.* **92**, 965-977.
- Shine, R., Olsson, M. M., Moore, I. T., LeMaster, M. P. and Mason, R. T.** (1999). Why do male snakes have longer tails than females? *Proc. R. Soc. B Biol. Sci.* **266**, 2147-2151.
- Snyder, R. C.** (1952). Quadrupedal and bipedal locomotion of lizards. *Copeia* **1952**, 64-70.
- Sumner, F. B. and Collins, H. H.** (1918). Autotomy of the tail in rodents. *Biol. Bull.* **34**, 1-6.
- Wake, D. B. and Dresner, I. G.** (1967). Functional morphology and evolution of tail autotomy in salamanders. *J. Morphol.* **122**, 265-305.
- Walker, C., Vierck, C. J. and Ritz, L. A.** (1998). Balance in the cat: role of the tail and effects of sacrocaudal transection. *Behav. Brain Res.* **91**, 41-47.
- Walter, R. M. and Carrier, D. R.** (2002). Scaling of rotational inertia in murine rodents and two species of lizard. *J. Exp. Biol.* **205**, 2135-2141.