

Integrative Biology of Tail Autotomy in Lizards*

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ABSTRACT

Self-amputation (autotomy) of the tail is essential for the survival of many lizards. Accordingly, it has garnered the attention of scientists for more than 200 years. Several factors can influence the release of the tail, such as the size, sex, and age of the lizard; type of predator; ecology; and evolutionary history of the lineage. Once lost, the tail will writhe for seconds to minutes, and these movements likely depend on the size and physiology of the tail, habitat of the lizard, and predation pressure. Loss of the tail will, in turn, have impacts on the lizard, such as modified locomotor performance and mechanics, as well as escape behavior. However, the tail is almost always regenerated, and this involves wound healing, altered investment of resources, and tissue differentiation. The regenerated tail generally differs from the original in several ways, including size, shape, and function. Here we summarize recent findings of research pertaining to tail autotomy, and we propose a framework for future investigations.

Introduction

Numerous strategies for evading predators have evolved among vertebrates, such as the C-start escape maneuver in fishes (Hale et al. 2002) and chemical defenses in mammals (Berenbaum 1995). For example, hedgehogs prey on toads and then smear the toxic secretions from the toads onto their spines (by mixing with saliva and licking; Brodie 1977). This toxicity by acquisition also occurs in the African crested rat, which gnaws and chews toxic trees and then smears the mixture onto specialized hairs (Kingdon et al. 2012). However, few examples of predator evasion are as dramatic as those that involve the shedding of a body part in the attempt to escape/survive. This ability, termed autotomy, essentially involves self-amputation (“auto-,” Greek “-self,” and “-tomy,” Greek “cutting or incision”). Widespread among vertebrates, it is not limited to one region of the body, involving limbs, skin, and the tail, depending on the species (Bauer and Russell 1992; Bely and Nyberg 2010). Several small mammals shed their tails when seized by a predator, initiating the loss by executing a whirling motion with the body (Sumner and Collins 1918). Among salamanders and newts (Amphibia: Caudata), both limbs and tails can be lost and regenerated (Wake and Dresner 1967; Bryant et al. 2002), with limb regeneration being unique to this group (Bryant et al. 2002). Reptiles often exhibit the ability to lose the tail during predator-prey interactions (Bellairs and Bryant 1985). Many snakes can lose a portion of their tail (e.g., Willis et al. 1982), and observations suggest that the lost tail can twitch repeatedly (Todd and Wassersug 2010). Tail loss commonly occurs in lizards, with the shed part often thrashing dramatically (Higham and Russell 2010). Regardless of what body part is lost, survival and, therefore, fitness are likely augmented (Bateman and Fleming 2009).

Tail autotomy in lizards has garnered the interest of scientists for more than 200 years (Hunter 1861; Poulton 1895; Longstaff 1907; Woodland 1920; Congdon et al. 1974). The importance of tail autotomy as a biological event is evidenced by the number of review articles dealing with this topic (Arnold 1984, 1994; Bellairs and Bryant 1985; Clause and Capaldi 2006; Bateman and Fleming 2009). However, we are still far from understanding the fundamental relationships between tail autotomy and fitness and also the mechanisms underlying various aspects of autotomy and regeneration. To date, studies have focused on the anatomy (Russell and Bauer 1992; Russell et al. 2001), ecological role (Vitt and Cooper 1986; Pafilis et al. 2009), energetics (Vitt et al. 1977; Fleming et al. 2009), evolution (Arnold 1984; Zani 1996), biomechanics (Higham and Russell 2010), neural control (Rumping and Jayne 1996; Higham and Russell 2010, 2012), and functional implications (Jusufi et al. 2008;

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Gillis et al. 2009; Kuo et al. 2012) of tail autotomy in lizards. It is clear that, based on this body of work, the tail is important for locomotion but is also effective in moving autonomously after the lizard has dropped it. In addition to the loss of the tail and the impact of this loss to the lizard, several studies have examined aspects of tail regeneration (Clause and Capaldi 2006; McLean and Vickaryous 2011). Recent examination of the leopard gecko *Eublepharis macularius* suggests that a latent period of scar-free healing is common following tail loss and that a blastema is critical for mediating regeneration (McLean and Vickaryous 2011).

Early observations of tail autotomy focused on key aspects of how tails are lost and how they behave once jettisoned. For example, Mahendra (1936) described the autotomized tail of *Hemidactylus* as twisting, writhing, and jumping about, purportedly mimicking the movements of an animal in pain. In addition, he noted that, even after activity subsided, tactile stimulus prompted the tail to resume its contortions (Mahendra 1936). The mechanisms underpinning these observations are not yet fully understood, but it is clear from more recent work that the underlying neural control of the tail muscles is complex and can lead to elaborate and vigorous movements that are activated only after detachment of the tail (Higham and Russell 2010, 2012). The revitalization of the motionless tail by physical contact indicates that sensory feedback is important for at least some of the movement of detached tails. However, almost nothing is known about the general role of sensory input in the modulation of the function of the released tail in squamates.

Several authors have reported on what triggers autotomy and what is required for the tail to be lost. For example, initial observations on tail autotomy in geckos suggested that it could not occur spontaneously in response to alarm. Instead, it was noted that a crucial condition of tail autotomy was that the tail be held a short distance posterior to the plane at which autotomy will occur, thereby providing a fulcrum about which the muscles can act (Woodland 1920). Subsequently, several authors noted that lizards can shed their tail without physical contact between the tail and the external stimulus (e.g., Bellairs and Bryant 1985). Despite these early observations, the mechanisms of tail loss remain inadequately studied and are discussed in greater detail below.

We first summarize the main points of the articles included in this special collection devoted to tail autotomy in lizards. Second, based on these wide-ranging contributions and the literature relating to caudal autotomy, we propose a framework for future studies by both highlighting key gaps in our understanding of tail autotomy and attempting to identify the potential for cross disciplinary and integrative studies (fig. 1).

Summaries of the Contributions in This Issue

The articles that constitute this collection cover a broad range of topics relating to caudal autotomy in lizards, and various

themes link the contributions together. The events related to caudal autotomy and regeneration follow a time course, and various questions can be posed along that trajectory. At the instant of tail loss, a dichotomy occurs (fig. 1), with the lizard and the detached tail each taking on independent roles and challenges. The lizard is faced with the task of regeneration of the lost appendage and of surviving in its absence, at least until regeneration is well established. The tail seemingly takes on the role of drawing the attention of a potential predator and of being successful at this for sufficiently long to allow the donor to escape. As such, the detached tail may display actions that never occur while it is attached to the body, exhibiting latent motor patterns being released by the act of separation.

The article by Higham et al. (2013) addresses the issue of tail movements and their roles immediately following autotomy. It does so by examining the kinematics, histochemistry, and physiology of the caudal musculature and by quantifying tail movements. The article begins by comparing the postautotomic activity of the tail of the leopard gecko with that of three other gekkotan species and considers the variation in frequency and amplitude of the tail movements in the context of the ecological circumstances in which each species lives. For all species examined, movements of the detached tail exhibit a combination of stereotyped and nonstereotyped movements that result in unpredictable patterns of motion that likely stimulate the visual centers of particular predators. The tail functions, after detachment, in an ischemic state and exhibits high endurance in an oxygen-deprived environment. Higham et al. (2013) characterize the work, power, fatigue properties, and performance characteristics of the caudal musculature of the detached original tail of the leopard gecko and compare these to those of the regenerate tail and a limb muscle (the iliofibularis). They note that the muscle of the original tail exhibits the slowest phenotype and is the most resistant to fatigue, with its slow oxidative fibers permitting sustained performance. When released, the speed of movement of the tail and the patterns of movement that it displays become more important than power, and the muscles of the original tail are well suited to these tasks. Future directions pointed to by this contribution include the examination of the movements of detached tails as they relate to the sensory perception and actions of natural predators and the effect of tail movements on the efficiency of escape from predation. More broadly, the detached tail is advocated as a vehicle for the study of neural circuitry and pattern generators and for the investigation of muscle fatigue and muscle physiology under ischemic conditions.

The contribution of Gilbert et al. (2013) deals with the other set of challenges that become immediately apparent upon detachment of the tail: those relating to triggering the regenerative response. Autotomy and regeneration are noted to be independent phenomena, and although usually thought of as being linked, their controls and triggers are separate. The responses and regeneration of the various tissue types that constitute the tail—skeletal, muscular, nervous, vascular, lymphatic, and integumentary—are described, and the role of the immune system in mediating successful regeneration is outlined. Following

in light of a number of hypotheses that address the likelihood of tail loss. The data are analyzed in two ways: for all 350 species combined and also by family (for those taxa with sufficiently abundant representation), the latter allowing phylogenetic effects to be more adequately examined. It is noted that relative tail length is affected by all of the factors examined, so that all tested hypotheses have some predictive value and there is considerable taxon-specific variability. Although it is noted that the amount of tail shed influences locomotor capabilities, it is pointed out that a certain portion of the tail might be lost without significant costs being incurred; this finding will have a significant impact on the concept of “economy of autotomy.” The authors conclude that the greatest costs of caudal autotomy are borne by larger, nocturnal, sit-and-wait predators that rely on crypsis to avoid predation. Future work is needed to test their findings and will require both laboratory and field investigations.

Investment in tail structure is investigated in a different way by Lynn et al. (2013). They explore the energetic costs of investment in a new tail once the original has been shed, employing as experimental subjects juvenile lizards that are still in their active growth phase. The questions posed are whether resources are preferentially directed toward the tail relative to the body, both when dietary resources become limiting and when the impact of these limiting resources is exacerbated by the energetic demands of growing a replacement tail. These questions are framed in the context of the concepts of compensatory growth (acceleration of the growth of a regenerating part at the expense of normal somatic growth) and life history strategy. Lynn et al. (2013) find that intact juvenile leopard geckos raised on low dietary rations exhibit no diminution in tail growth when compared to high diet controls, even though these conditions negatively impact body growth. Tail loss and regeneration impose further limitations on body growth rates, whereas tail growth rates are accelerated. Compensation for providing the energy needed to promote tail growth is achieved by directing energy away from body growth (which proceeds at a slower pace) and likely by reduction in metabolic activity because animals regenerating their tails did not consume more food than did their control comparators. For juvenile leopard geckos, tail growth is a priority following autotomy. This may be so because this species is long-lived and fat tailed and investment in the tail may be crucial for assuring reproductive success once sexual maturity is attained. How widespread such responses are remains unknown. It appears, however, that there may be ontogenetic shifts in priorities within the same species. Tail type and foraging mode (as pointed out in Fleming et al. 2013) may influence the propensity for compensatory growth. Lynn et al. (2013) note that the life history consequences of caudal regeneration require considerably more study.

McElroy and Bergmann (2013) investigate another aspect of the potential costs of tail loss and focus on locomotor performance as it relates to fitness. Maximum sprint speed and maximum acceleration are employed as measures of the impact of autotomy on locomotor performance. As was done by Fleming et al. (2013), relative tail length is examined as a variable, along

with tail volume and body volume. The available data indicate that the majority of lizard species incur a negative impact on maximum sprint speed when the tail is lost. A smaller proportion exhibits no effect, and even fewer are influenced positively. Overall, the outcome is that the relatively bigger the tail, the greater the negative impact on sprint speed. Tail volume (and thus mass) explains more of this effect than tail length, an interesting outcome that bears comparison with the findings of Fleming et al. (2013) and Lynn et al. (2013). Various possible reasons for this association are explored, and it is noted that in a similar vein to the findings of Fleming et al. (2013), there are likely strong phylogenetic effects associated with particular regions of the lizard phylogenetic tree. The authors ponder the variation evident in their data and suggest that performance traits other than sprint speed and acceleration are likely to be of importance and should be considered further. It is noted that the biomechanics of locomotion following autotomy are not well known and that the application of approaches such as force plate recording, kinematic analysis, and electromyography will help elucidate such matters, a theme that is also taken up by Gillis et al. (2013; see below). McElroy and Bergmann (2013) note that, to date, sampling of lizards in relation to locomotor performance has been rather random, and they suggest that more focused investigation within single clades will likely clarify certain issues. They propose that such investigations will benefit from concurrent investigation of multiple aspects of performance.

The kinematic effects of autotomy are addressed by Gillis et al. (2013). They note that jumping is routinely employed by arboreal lizards as a means of navigating their habitat and that little is known of the impact of caudal autotomy on this behavior. When a lizard loses its tail, all specialized function(s) that the tail has are forsaken, and Gillis et al. (2013) ask whether lizards can compensate for the equilibrium-inducing properties of the tail following its loss. They indicate that recent work has quantified the role of the lizard tail as an in-air stabilizer and employ this insight to undertake a series of experiments that explore the effectiveness of jumping in green anoles when faced with varying degrees of tail loss. In so doing, they discover that the loss of the tail has a major impact on jump trajectory and stability, although it does not affect takeoff velocity or jump distance. Physical interaction of the tail with the substratum during the takeoff phase of the jump moderates trajectory and body posture, and in its absence these are disrupted. Subsequent experiments investigate the impact of tail loss on jumping to targets above and below the takeoff point. A great deal of individual variation is noted, but an association between an increasing amount of tail lost and an increased amount of posterior rotation of the body is revealed. Compensation for tail loss through increased experience was shown not to occur, indicating that the effects on jumping induced by tail loss may be long term rather than temporary. Whether this is the case for the aspects of locomotor performance examined by McElroy and Bergmann (2013) remains to be investigated. The extensive individual variation that these authors noted led them to conclude that the impact of tail loss may be quite different for

different individuals, and thus, it may be a powerful agent of selection. Gillis et al. (2013) note the need for more sophisticated approaches to understanding the biomechanical impacts of caudal autotomy on locomotor function, thus echoing the sentiments of McElroy and Bergmann (2013). It is evident that the fitness consequences of caudal autotomy need to be assessed through detailed laboratory and field observations.

Future Directions

Each contribution to this special collection reveals major gaps in our understanding of tail autotomy. With these in mind, we elaborate on five key areas of research for which there is a paucity of information and that will lead to significant advances in our understanding of the integration of events and phenomena associated with caudal loss and regeneration (fig. 1). In so doing, we emphasize the need for integrative analyses of tail autotomy. Only with such approaches will we begin to understand the mechanisms underlying tail autotomy and the evolution of its diversity.

Evolution of Tail Autotomy

Caudal autotomy appears to be the ancestral condition among Lepidosauria. Although the evolution of tail autotomy has been examined (Arnold 1984; Zani 1996), there are a number of remaining questions that can now be addressed using robust phylogenies that are continually being improved because they are based on ever-increasing amounts of molecular and morphological information (Wiens et al. 2012; Pyron et al. 2013). Questions that immediately arise include that of how many times, and under what conditions, the ability to undergo tail autotomy has been lost (and regained) in lizards. Given that the loss of autotomy has surely occurred in several groups independently (e.g., in the Phrynosomatidae [*Phrynosoma*], Chamaeleonidae, and Tropicuridae [*Uracentron*]), we can examine the mechanisms underlying this convergence and ask whether there are common selective pressures that drive the loss of the ability to autotomize the tail. Such findings can also be compared to ontogenetic trajectories that result in the loss of autotomic ability as a function of growth in certain species, such as for many species of the Iguanidae (Arnold 1984). In addition to repeated losses, there appear to be independent gains of autotomy from ancestors that lack it. These secondary origins tend to involve intervertebral planes as the sites of autotomy rather than the ancestral intravertebral planes (Bellairs and Bryant 1985).

Future research should elucidate the evolution of a range of traits relevant to caudal autotomy rather than focusing solely on fracture planes. For example, the ability to lose a tail, the ease of autotomy, and the ability to regenerate are traits that have not yet been examined within a phylogenetic framework. In addition to predation, the evolutionary role of social structure in determining various aspects of tail autotomy has not been examined. Given the incredible phenotypic diversity

among the tails of different species of lizard, the evolution of tail anatomy is something that also needs to be addressed.

Ecology and Ethology of Tail Autotomy

There is some circumstantial evidence that ecological factors, such as habitat structure and temperature, have an impact on tail autotomy (reviewed in Arnold 1994). However, the lack of accounting for phylogenetic history means that there is little evidence that habitat structure is directly linked to the ease of autotomy. One aspect that we do not fully understand is the differential role of the tail in different habitats across the spectrum of lizard species. Although some groups, such as chameleons, have a prehensile tail that is clearly functionally and mechanically important in arboreal locomotion (Higham and Anderson 2013), the details of tail function in other arboreal lizards are not well understood. In addition, some lizards with prehensile tails, such as species of *Elgaria* and *Abronia*, readily autotomize their tails. The impact of tail loss for these species would appear to be significant, although little is known about the trade-offs between tail autotomy and locomotion in these lizards. Although it is easy to make a case that tails are important for climbing, evidence appears to suggest that climbing species relinquish their tails more easily than do ground dwellers (Arnold 1994). This is an area in which more extensive research is necessary. As noted by Arnold (1994), we lack a suitable measurement of tail fragility, which is necessary for comparing among and between ecological categories, although there have been attempts to determine the pinching force necessary to stimulate autotomy (Fox et al. 1998).

In addition, the impacts of habitat structure (and other ecological factors) on the postautotomic movement patterns of tails are completely unknown. Although some information suggests that climbing species are more likely to drop their tail, it seems that terrestrial species might gain more from postautotomic movements. If the goal is to distract a predator for sufficient time to enable escape, then tail movements would be more effective for an animal living on the ground. In an arboreal or rocky habitat, where climbing is more important, an amputated tail will potentially fall farther and be less influential during the predator-prey interaction. These potential scenarios must be tested in a phylogenetic framework.

The behavior of lizards immediately following the autotomy of their tail also appears to be quite variable. In fact, escape strategies can change completely when the tail is no longer present. The skink *Sphenomorphus quoyii* usually escapes from predators by jumping into water and swimming, using its tail as the propulsive device. However, a tailless individual is more likely to flee on land or hide submerged on the bottom of water courses (Daniels 1985). It is therefore possible that tail autotomy has widespread impacts on the ecology of an animal. This alteration of ecological interactions, even if only for a relatively short period of time, will change selection pressures and potentially have a great influence on fitness. The impact of autotomy can also affect performance under some conditions but not others. In a study of the Cape dwarf gecko (*Lygodactylus*

capensis), tail autotomy was found to significantly affect escape speed on an inclined surface but not a horizontal surface (Medger et al. 2008). This highlights the need to consider ecological conditions, such as habitat structure, when assessing the impacts of tail autotomy. Future work detailing the effects on ecology and fitness will provide valuable information regarding the costs and benefits associated with autotomy.

Several questions regarding the role of ecology in the biology of tail autotomy remain elusive. What actually occurs, with respect to the tail, during predator-prey interactions? If tail loss permits survival, how often does it actually work? Do writhing tails actually distract predators, or does the tail simply provide something to eat? How does habitat structure relate to tail autotomy and to the behavior of the tail following autotomy? Such questions regarding the ecology and ethology of caudal autotomy are of great importance and should be addressed in future work. There are definitely cases in which tail autotomy has been demonstrated to permit the lizard to flee from a predator, such as that during an attack by the king snake (*Lampropeltis triangulum*) on the skink *Scincella lateralis* (Dial and Fitzpatrick 1983, 1984). Such data, however, are scarce. Field observations would be ideal, but one problem is that the predators of lizards are often snakes, which generally do not need to eat frequently. Thus, it will be challenging to be able to observe sufficient interactions between snakes and lizards and even harder to observe tail autotomy during these interactions. A promising technique is field video recording that can be triggered using security surveillance technology (Clark et al. 2012). In this way, predatory strikes of snakes on lizards could be observed, and the outcome could be related to tail autotomy.

Physiology of Tail Autotomy

How does the amputation of the tail during autotomy actually occur? How do the muscles act to divide a vertebra? Is autotomy dependent on physical contact posterior to the plane of autotomy, and, if not, how is the tail released in the absence of such contact? What is the neural network that controls the movements of the tail following autotomy? These questions constitute an exciting area for future work at the interface between physiology and autotomy. As noted by Bellairs and Bryant (1985), the precise method of autotomy likely differs between species, although our understanding of the mechanics is simply far too limited to even make predictions. The forces required to amputate the tail are also likely dependent on the species and the conditions at the time of autotomy. A contributory role for the fat within the tail to the mechanics of autotomy has also been proposed, but this requires further investigation (Sheppard and Bellairs 1972).

Tail Regeneration

Although several studies have examined the mechanisms and anatomy of regeneration, little attention has been given to the function of the regenerated tail. When/if the replacement is autotomized, does it act like the original? How does a regen-

erated tail function in an animal that uses the original tail during locomotion, as is the case for some arboreal lizards? It is clear from anatomical studies that the regenerated tail is structurally different from the original (Bellairs and Bryant 1985; Alibardi 2010). However, the number of species for which this information exists is quite small, and it is possible that the regenerated tail may be quite differently proportioned and structured in others.

Autotomy and regeneration occur in some species that appear to utilize the tail substantially during locomotion, such as the prehensile tail of alligator lizards (*Elgaria* and/or *Gerrhonotus*). Although we do not completely understand the impacts of autotomy in these groups, it appears that the tail is extremely important when attached to the animal and when it is lost. This system provides a rich framework for addressing questions regarding trade-offs, given the ostensible importance of the tail in both of these behaviors (during locomotion and immediately after autotomy). In addition, the function of the regenerated tail might be a critical aspect of survival in these lizards. One might expect that regeneration occurs more rapidly in those species that rely on their tail for locomotion and that the function of the regenerated tail more closely matches original function in such situations.

Other questions relating to regeneration will tackle the process itself and will have biomedical as well as strictly biological implications (Alibardi 2010; Delorme et al. 2012). The lizard tail provides the best amniote model of regeneration and straddles the divide between mammals, which display poor regenerative capacity, and nonamniote vertebrate models (salamanders and fish), which exhibit almost perfect regenerative capacities (McLean and Vickaryous 2011). As the process of regeneration becomes more completely understood, important comparative aspects will emerge (Tanaka and Ferretti 2009) that will assist in the quest to promote more effective and complete regeneration in humans. The regenerating lizard tail will likely increase in prominence as a vehicle to address fundamental questions relating to epimorphic regeneration. The establishment of staging tables for caudal regeneration (McLean and Vickaryous 2011) for lizards exhibiting different patterns and forms of the tail will enable the selection of different species for specific questions, such as those that follow. What molecular mechanisms are responsible for the production of fully functional regenerated systems? What regulates tissue differentiation and structuring? What factors permit full differentiation of certain tissues but prevent others (such as lymphangiogenesis vs. neurogenesis; Daniels et al. 2003; Tanaka and Ferretti 2009)?

Ontogeny of Tail Autotomy

Not all autotomic events are equal. Small lizards likely benefit more from autotomy, given their vulnerability to predators. Larger species (or individuals) are also better suited to stand their ground and fend off a predator, so losing their tail may be less imperative for survival. Finally, a larger lizard has likely invested relatively more in its tail than has a smaller one, thus rendering the tail more important (energetically). Obviously,

size differences occur within a species throughout ontogeny, as well as between species, suggesting that size may have an impact at multiple levels. Future work that systematically explores the implications of ontogeny for the biomechanics, regeneration, energetics, and ecology of lizards with and without having undergone autotomy will enable us to tease apart the role and importance of size, which is likely a key factor in the evolution of tail function.

Conclusions

Tail autotomy and the subsequent movement of that tail constitute innovations that facilitate escape from a predatory attack (among other things). Our understanding of tail autotomy in lizards has progressed considerably over the past 3 decades. The following special collection of articles has advanced the understanding of tail autotomy by integrating cutting-edge topics, and it has provided a framework on which to build. These articles have examined the dynamics of the tail moving after autotomy, the movement of the animal after losing the tail, and the processes associated with regenerating a tail. Even so, there remain numerous questions that are as yet unanswered, and little is known about the causes of phenotypic diversity (morphology, physiology, and behavior). The overview presented here is meant to highlight key aspects of tail autotomy that are critical for the evolution and ecology of lizards but that remain poorly understood. How lizards escape from predators, capture prey, deal with complex habitat structure, and interact with other lizards are all likely dependent on tail autotomy and subsequent regeneration. Thus, this is a fundamental aspect of lizard biology that demands further investigation. In addition, applications related to tail autotomy are continually emerging, including topics such as regenerative medicine and spinal cord injury. With the infusion of new research and the incorporation of cutting-edge techniques, we are on the verge of defining new conceptual boundaries within the field of tail autotomy.

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