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Is partial tail loss the key to a complete understanding of caudal autotomy?

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Abstract Autotomy, the self-amputation of limbs or appendages, is a dramatic anti-predator tactic that has repeatedly evolved in a range of invertebrate and vertebrate groups. In lizards, caudal autotomy enables the individual to break away from the predator's grasp, with the post-autotomy thrashing of the tail distracting the attacker while the lizard makes its escape. This drastic defensive strategy should be selectively advantageous when the benefit (i.e. survival) exceeds the subsequent costs associated with tail loss. Here, we highlight how the position of autotomy along the length of the tail may influence the costs and benefits of the tactic, and thus the adaptive advantage of the strategy. We argue that most studies of caudal autotomy in lizards have focused on complete tail loss and failed to consider variation in the amount of tail shed, and, therefore, our understanding of this anti-predator behaviour is more limited than previously thought. We suggest that future research should investigate how partial tail loss influences the likelihood of surviving encounters with a predator, and both the severity and duration of costs associated with caudal autotomy. Investigation of partial autotomy may also enhance our understanding of this defensive strategy in other vertebrate and invertebrate groups.

Key words: anti-predator behaviour, economy of autotomy, locomotor performance, squamate reptile, tail autotomy, trade-off.

CAUDAL AUTOTOMY AS A DEFENSIVE STRATEGY

As an individual's ability to avoid predation is essential for its continued survival, anti-predator behaviours are generally under strong selection (Edmunds 1974; Lima & Dill 1990; Ferrari *et al*. 2009). This has led to a remarkable diversity of defensive tactics to enable animals to evade (e.g. crypsis, camouflage, mimicry) or escape from a predator (e.g. fleeing, group defence, chemical secretions) (Edmunds 1974; Mallet & Joron 1999), including some seemingly bizarre strategies (e.g. spiny, projectile ribs in salamanders; Heiss *et al*. 2010). Autotomy, the capacity to 'voluntarily' shed a limb or appendage, is a dramatic anti-predator behaviour that has evolved independently in numerous invertebrate (e.g. insects, spiders, crustaceans, echinoderms; Maginnis 2006; Fleming *et al*. 2007) and vertebrate groups (e.g. fishes, amphibians, squamate reptiles, mammals; Bernado & Agosta 2005; Caro 2005; Bateman & Fleming 2009). However, autotomy has been most widely studied in lizards where caudal autotomy occurs in at least 13 of the 20 recognized families (Downes & Shine 2001; Bateman & Fleming 2009).

There are two main components of caudal autotomy in lizards: breaking away from the predator's grasp, and distracting the attacker to facilitate its escape (Arnold 1988; Bateman & Fleming 2009). Tail loss is a last ditch tactic that is usually only employed after the frontline defensive behaviours (e.g. crypsis, fleeing) have failed (Arnold 1984, 1988; Clause & Capaldi 2006; Bateman & Fleming 2009). If an attack is directed towards the tail, caudal autotomy may allow the lizard to escape from the predator's grip. However, breaking free from the predator is simply the first part of a strategy that ultimately requires the lizard to reach a secure refuge site (Arnold 1988). In most species the shed tail writhes and thrashes and acts to confuse or distract the predator while the tailless lizard makes its getaway (Arnold 1984, 1988; Bateman & Fleming 2009). As autotomy is under neurological control, lizards are also capable of pre-emptively detaching their tails before they are grasped (i.e. when a predator attack is imminent), thereby dividing the predator's attention and leaving it with the option of pursuing the lizard or eating the shed tail (Arnold 1988; Bateman & Fleming 2009). The majority of lizard species that employ caudal autotomy are subsequently capable of completely regenerating their tails (Bellairs & Bryant 1985; Arnold 1988; Clause & Capaldi 2006; Bateman & Fleming 2009).

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THE SELECTIVE ADVANTAGE OF TAIL LOSS DEPENDS ON THE BALANCE BETWEEN ITS COSTS AND BENEFITS

The benefit of caudal autotomy is clear: surviving a potentially fatal encounter with a predator (Arnold 1984, 1988; Bateman & Fleming 2009). However, the subsequent consequences of discarding a valuable appendage may be complex, severe and long-lasting. The costs associated with tail loss in lizards may stem from four different factors (Bateman & Fleming 2009):

1. The absence of the tail

Tailless lizards are no longer able to use autotomy as a defensive tactic and are less likely to survive subsequent predatory encounters (Congdon *et al.* 1974; Daniels 1985; Downes & Shine 2001). Locomotor performance is usually impaired following caudal autotomy (Chapple & Swain 2002a; Chapple *et al.* 2004; Lin & Ji 2005; Lin *et al.* 2006; Cooper & Smith 2009; Cromie & Chapple 2012), and tailless lizards may experience reduced social status (Fox & Rostker 1982; Fox *et al.* 1990).

2. The loss of energy reserves that are stored in the tail

Many lizard species store a substantial proportion of their lipid reserves in their tail, some of which may be jettisoned along with the shed tail (Chapple & Swain 2002b; Doughty *et al.* 2003; Lin *et al.* 2006; Sun *et al.* 2009).

3. The energy and resources required to replace the tail

It is energetically expensive to regenerate the tail and may necessitate the diversion of resources previously allocated to growth, reproduction and general maintenance (Smith 1996; Wilson & Booth 1998; Chapple *et al.* 2002; Chapple & Swain 2004a).

4. Indirect impacts on habitat use and behaviour

Tailless lizards may modify their habitat use, home ranges, foraging behaviour, anti-predator behaviour and basking site selection (Martin & Salvador 1992, 1993, 1995, 1997; Downes & Shine 2001; Cooper 2003, 2007; Cooper & Wilson 2008, 2010).

More than two decades ago, Arnold (1988) emphasized that in order for caudal autotomy to be selectively advantageous, the benefit needs to exceed the costs associated with tail loss. While there have been substantial advances in our knowledge of the costs stemming from tail loss since Arnold's influential review (reviewed in Bateman & Fleming 2009), we argue that there remains a critical gap in our understanding of the adaptive advantage of caudal autotomy in lizards. This is because not all tail loss is equivalent, and the length of tail shed not only influences the likelihood that the lizard will escape from the predator (Daniels 1985; Cooper & Smith 2009), but also the severity and duration of costs that are incurred (Downes & Shine 2001; Chapple & Swain 2002a,b; Lin & Ji 2005; Lin *et al.* 2006; Sun *et al.* 2009). Here we demonstrate that the ability for partial tail loss to shift the balance between the costs and benefit of caudal autotomy in lizards has been largely overlooked.

WHY IS A GREATER FOCUS ON PARTIAL TAIL LOSS REQUIRED?

Given its ability to alter the costs and benefits of tail loss, we sought to determine how regularly variation in the length of tail shed is considered in studies of caudal autotomy in lizards. Relevant papers were identified through a Web of Science search (search terms: lizard AND tail loss, lizard AND autotomy) and from the reference lists of the main review papers in the field (Arnold 1984, 1988; Clause & Capaldi 2006; Bateman & Fleming 2009). Here we examine 98 studies that have investigated the costs and benefits of caudal autotomy in lizards (Appendix S1).

Tail autotomy occurs through fracture planes within caudal vertebrae (i.e. intravertebral autotomy) and the surrounding musculature, blood vessels and soft tissues (Bellairs & Bryant 1985; Bateman & Fleming 2009). Apart from some exceptions (e.g. several diplodactylid and gekkonid geckos, some iguanids), lizard species that are capable of autotomy have fracture planes within the majority of their caudal vertebrae and are therefore able to detach their tail at any point along its length (Arnold 1984, 1988; Bellairs & Bryant 1985; Bateman & Fleming 2009). During encounters with a predator, the tail break generally occurs a few vertebrae more proximal to where the lizard is grasped by its attacker (Bateman & Fleming 2009). This acts to limit the amount of tail shed during autotomy, and has been referred to as 'economy of autotomy' (Arnold 1988). Almost half of the studies (16 of 35, 45.7%) that have examined the incidence of tail autotomy in natural lizard populations have investigated the position along the length of the tail where the breaks occurred (Appendix S1). In most species that have been examined, complete tail autotomy appears to be relatively rare compared with partial tail loss (Chapple & Swain 2002b, 2004b; Lin & Ji 2005; Bateman & Fleming 2011).

Losing only a portion of the tail decreases the likelihood that autotomy will result in the reduction of

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energy reserves (Chapple & Swain 2002b; Doughty *et al.* 2003), and minimizes the amount of tail that needs to be regenerated. Some costs of tail loss, such as reduced locomotor performance, may only be evident when more than half of the tail is autotomized (Lin *et al.* 2006; Cooper & Smith 2009; Sun *et al.* 2009). In addition, most costs associated with caudal autotomy are transient and persist only until the tail is regenerated beyond a certain threshold length (e.g. half the original tail length; Downes & Shine 2001; Chapple & Swain 2002a; Lin *et al.* 2006). However, the vast majority of laboratory-based studies (58 of 67, 86.6%) have focused solely on the impact of autotomy following the inducement of complete tail loss (Appendix S1). The tendency for researchers to experimentally remove the complete tail has been noted previously in the context of the reproductive costs of autotomy (Bernado & Agosta 2005), but has yet to be explored in relation to how the length of tail lost may influence both the severity and duration of costs following autotomy. Indeed, only a fraction of studies have considered whether the impact of autotomy is related to the amount of tail shed (nine of 62, 14.5%), or determined the duration of the costs associated with caudal autotomy (five of 55, 9.1%) (Appendix S1).

Although economy of autotomy may be an effective tactic for reducing the costs associated with tail loss, partial tail loss might not be sufficient to distract the predator and allow the lizard to escape (Arnold 1988). The vigour and duration of post-autotomy tail movement acts to increase the time taken for predator's to handle and consume the shed tail (Arnold 1988), and longer tail portions may writhe more violently than shorter segments (Cooper & Smith 2009). However, only one study (Cooper & Smith 2009; one of 13, 7.7%) has investigated whether intraspecific variation in shed tail lengths influences post-autotomy tail movement (Appendix S1). In the speckle-lipped mabuya (*Trachylepis maculilbris*) longer tail segments moved further than shorter ones, but there was no relationship between the movement duration and the length of the tail portion. Similarly, only a single study (Daniels 1985; one of 10, 10%) has examined whether the amount of tail autotomized during a predatory encounter influences an individual's probability of survival (Appendix S1).

CONCLUSIONS

We argue that because of a tendency for researchers to overlook the influence that partial tail loss can have on both the costs and benefits (ability to distract a predator) associated with caudal autotomy, our understanding of the adaptive significance of this defensive strategy is actually more limited than previously believed. To address this situation, future research should focus on how the position of tail autotomy, and length of the shed tail, influences the probability of survival during predatory encounters and the presence, severity and duration of potential costs associated with the tactic. Indeed, some recent studies have adopted an approach similar to that advocated in this article and have specifically investigated how variation in the position of autotomy influences the costs and benefits associated with tail loss (Lin & Ji 2005; Lin *et al.* 2006; Cooper & Smith 2009; Sun *et al.* 2009). The accumulation of similar studies will enhance our understanding of the dynamic balance between the costs and benefits of caudal autotomy and may ultimately enable us to comprehend why the strategy is so widespread in some species and taxonomic groups, but reduced or secondarily lost in others (e.g. Arnold 1984, 1988; Bateman & Fleming 2009).

In addition, we believe that the investigation of partial autotomy has the potential to enhance our broader understanding of the adaptive significance of this defensive tactic in other vertebrate and invertebrate groups. Although the body part that is autotomized may vary between taxonomic groups (e.g. leg, arm, tentacle, antennae, caudal lamellae), the break invariably occurs through a fracture plane and is under central control (i.e. neural or hormonal) (reviewed in Maginnis 2006; Fleming *et al.* 2007). While the capacity for partial autotomy is limited in some groups because of presence of only a single fracture plane, variation in the amount of appendage shed is evident in several groups (e.g. spiders, echinoderms, salamanders; Marrs *et al.* 2000; Bernado & Agosta 2005; Fleming *et al.* 2007). Given that the costs associated with autotomy in most groups mirror those seen in lizards (e.g. impaired locomotor performance, modified behaviour, reduced reproduction, altered antipredator tactics, decreased survival), and these costs are incurred until the appendage is regenerated (Bernado & Agosta 2005; Maginnis 2006; Fleming *et al.* 2007), variation in the length of the appendage shed may shift both the costs and benefits that result from the strategy. Thus, autotomy in animals should not be viewed as an 'all or nothing' behaviour, but as a flexible defensive tactic where the balance between the resultant costs and benefits is determined by the length of the appendage that is shed.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Summary of 98 studies examining the benefits and costs of tail loss in lizards.

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