

The ecology and evolution of autotomy

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ABSTRACT

Autotomy, the self-induced loss of a body part, occurs throughout Animalia. A lizard dropping its tail to escape predation is an iconic example, however, autotomy occurs in a diversity of other organisms. Octopuses can release their arms, crabs can drop their claws, and bugs can amputate their legs. The diversity of organisms that can autotomize body parts has led to a wealth of research and several taxonomically focused reviews. These reviews have played a crucial role in advancing our understanding of autotomy within their respective groups. However, because of their taxonomic focus, these reviews are constrained in their ability to enhance our understanding of autotomy. Here, we aim to synthesize research on the ecology and evolution of autotomy throughout Animalia, building a unified framework on which future studies can expand. We found that the ability to drop an appendage has evolved multiple times throughout Animalia and that once autotomy has evolved, selection appears to act on the removable appendage to increase the efficacy and/or efficiency of autotomy. This could explain why some autotomizable body parts are so elaborate (e.g. brightly coloured). We also show that there are multiple benefits, and variable costs, associated with autotomy. Given this variation, we generate an economic theory of autotomy (modified from the economic theory of escape) which makes predictions about when an individual should resort to autotomy. Finally, we show that the loss of an autotomizable appendage can have numerous consequences on population and community dynamics. By taking this broad taxonomic approach, we identified patterns of autotomy that transcend specific lineages and highlight clear directions for future research.

Key words: animals, anti-predatory trait, appendage loss, autotomy phenotype, interspecific comparisons, limb loss, predation, prey, regeneration, tail loss.

CONTENTS

I. Introduction	1882
II. A working definition of autotomy	1882
III. Evolution of the autotomy phenotype	1883
(1) Evolutionary origins and losses of autotomy	1883
(2) Elaboration of autotomizable appendages	1883
IV. Variation in the costs and benefits of autotomy	1885
(1) Benefits of autotomy	1885
(2) Costs of autotomy	1887
V. Economic theory of autotomy: predicting when an individual should autotomize	1889
VI. Implications of autotomy on organismal and environmental interactions	1891
(1) Predator–prey interactions	1891
(2) Intraspecific competition	1891
(3) Movement and habitat selection	1892
VII. Applications of autotomy research	1892
VIII. Future directions	1892
IX. Conclusions	1893
X. Acknowledgments	1893
XI. References	1893
XII. Supporting Information	1896

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I. INTRODUCTION

A lizard dropping its tail to escape predation dramatically illustrates the importance of survival in the context of natural selection, which is why autotomy (i.e. self-induced loss of a body part) has become a textbook example of an anti-predatory trait (Goodenough, McGuire, & Jakob, 2009). This example, however, does not capture the full diversity of organisms that use autotomy, the variety of body parts that can be dropped, nor the subtler nuances of autotomy, such as the range of ecological contexts under which autotomy can occur. In addition to lizards, autotomy has been observed in several other lineages, including cephalopods, arthropods, and salamanders (Wake & Dresner, 1967; Fleming, Muller, & Bateman, 2007; Bush, 2012). Phylogenetic comparative analyses – including analyses conducted for this review – reveal that autotomy has multiple evolutionary origins, as well as losses (Zani, 1996). The diversity of organisms that autotomize is mirrored in a diverse array of autotomizable appendages. Examples include tails, claws, and legs (Wake & Dresner, 1967; Fleming *et al.*, 2007). These autotomizable structures are often more elaborate (e.g. larger in size, have more conspicuous colouration) than homologous structures that cannot be dropped (Arnold, 1984; Fleming, Valentine, & Bateman, 2013), which suggests that having the ability to drop a limb may facilitate trait diversification. The first of three objectives of this review is to synthesize our current understanding of the evolution of autotomy and the elaboration of autotomizable appendages (i.e. synthesize the evolution of the autotomy phenotype).

In addition to being an extreme anti-predatory trait, autotomy can be beneficial in a variety of other contexts, and sacrificing a limb may not always be as costly as it is often assumed. Autotomy is also used to escape non-predatory entrapment (Maginnis, 2008), reduce the cost of injury (Emberts *et al.*, 2017), and increase an individual's reproductive success. Some male spiders, for example, have been observed autotomizing part of their intromittent organs (an external structure used to transfer sperm) inside a female's reproductive tract (Fromhage & Schneider, 2006; Uhl, Nessler, & Schneider, 2010), which can ultimately increase the male's reproductive success (Snow, Abdel-Mesih, & Andrade, 2006). Complete loss of these intromittent organs may result in the male becoming functionally sterile, which highlights the extreme costs that can be associated with autotomy. However, these costs can vary dramatically from one organism to the next. For example, harvestmen can lose up to two legs before experiencing any notable costs to locomotion (Guffey, 1999). The second objective of this review is to synthesize our current understanding of the costs and benefits associated with autotomy. Given such variation in the cost to benefit ratio, we also modified the economic theory of escape (Ydenberg & Dill, 1986) to generate an economic theory of autotomy, which makes predictions about when an individual should autotomize.

Loss of an autotomizable appendage can also affect how an individual interacts with other organisms and its environment. For example, male Iberian rock lizards (*Iberolacerta monticola*) reduce their home-range size following tail autotomy, which has implications for reproductive opportunity (Salvador, Martín & López, 1995). Loss of an autotomizable appendage can also affect an organism's foraging behaviour and success. Asian shore crabs (*Hemigrapsus sanguineus*) missing both of their chelipeds, for example, have a slower feeding rate and consume smaller prey items than do intact individuals (Davis *et al.*, 2005). This altered pattern of foraging behaviour and feeding success highlights that autotomy may have a cascading effect on community dynamics, especially when one considers that 16% of the observed population is missing at least one cheliped. The final objective of this review is to synthesize our current understanding of the ecological implications of autotomy.

This review does not provide a comprehensive taxonomic overview of autotomy nor does it directly discuss autotomy in relation to regeneration. We intentionally avoided these topics because we believe that they have already received a good amount of attention. For taxonomic specific reviews of autotomy see McVean (1975), Arnold (1984), Juanes & Smith (1995), Wilkie (2001), Fleming *et al.* (2007, 2013), Bateman & Fleming (2009), Higham, Russell, & Zani (2013). For previous reviews on the relationship between autotomy and regeneration see Wilkie (2001), Maginnis (2006) and Bely & Nyberg (2010). Because autotomy and regeneration are often coupled, we do consider some implications of regeneration. However, it is important to note that regeneration does not always succeed autotomy, and in many cases the loss of an appendage is permanent.

II. A WORKING DEFINITION OF AUTOTOMY

One of the largest obstacles surrounding the study of autotomy is defining it. Since it was first coined (Fredericq, 1883), 'autotomy' has generally been used to denote a conscious decision on the part of an organism to drop an appendage, usually at a specific plane and often as a defence against predators. Herein, we simply define autotomy as the self-controlled loss of a body part at a predetermined breakage location. Therefore, as long as detachment consistently occurs at one, or in some cases multiple, predetermined fracture planes across a population, we consider the self-controlled loss of a body part to be autotomy. To differentiate autotomy from moulting/shedding, we also specify that autotomy should not be restricted to a certain climatic season or transitional period during development. We find this purely descriptive definition to be suitable for numerous reasons. First, autotomy has additional benefits beyond that of escaping predation, thus whether an individual uses autotomy in an anti-predatory context should not be incorporated into the definition. Second, by removing adaptive benefits from the

definition, we can also begin to move away from a purely adaptive perspective and therefore broaden our scope, and hopefully our understanding, of autotomy. This definition, for example, allows us to investigate other adaptive [e.g. increased reproductive success (Ghislandi, Bilde, & Tuni, 2015)] and non-adaptive [e.g. phylogenetic inertia (Van Sluys, Vrcibradic, & Rocha, 2002)] hypotheses for observing self-induced appendage loss.

III. EVOLUTION OF THE AUTOTOMY PHENOTYPE

(1) Evolutionary origins and losses of autotomy

The number and diversity of species that can undergo autotomy is quite remarkable. This diversity alone suggests that autotomy has evolved independently multiple times. In fact, it is widely accepted that autotomy has more than one evolutionary origin (McVean, 1975). However, no study has provided evidence for this claim. This discrepancy is likely due to the absence of a study that has mapped autotomy onto a phylogenetic tree of Animalia, which, to gain a broad overview of autotomy's evolutionary history, we present in Fig. 1 (see online Supporting Information, Appendix S1 and Figure S1). Although it is difficult to calculate the exact number of times autotomy has evolved independently, identifying whether autotomy has more than one evolutionary origin is relatively simple. Therefore, we conducted stochastic character simulations to estimate the number of times autotomy has evolved and found that autotomy has at least nine independent origins across Animalia (Appendix S1). Despite having multiple origins, much remains unknown about the evolution of autotomy as there have been no studies that have implemented experimental evolution and there have been only a handful of studies that have explicitly investigated autotomy within a phylogenetic framework (Zani, 1996; Mueller *et al.*, 2004; implicit studies include Bateman & Fleming, 2008; Pafilis *et al.*, 2009). Of the phylogenetic studies, autotomy is always found to be the ancestral character of the investigated clade, but there are often multiple secondary losses [i.e. there are species that are unable to autotomize nested within the clade (Zani, 1996; Mueller *et al.*, 2004)]. As a result, most research on the evolution of autotomy has investigated factors that correlate with its secondary loss.

Two factors observed to correlate with a reduction in the ability to autotomize across species are (i) body size, and (ii) the function of the autotomizable body part, but there is conflicting evidence. In orthopterans, larger species take longer to autotomize their hind limbs (Bateman & Fleming, 2008). This across-species correlation, however, does not hold for lizards (Zani, 1996), as there is no correlation between the frequency of tail loss in natural populations – a fair proxy for the latency to autotomize in this clade (Pafilis *et al.*, 2009) – and body size (Zani, 1996). Since adult orthopterans cannot regenerate their autotomized body part,

while lizards can, these differing patterns could potentially be explained by regeneration. With regards to the function of the autotomizable body part, the inability to autotomize a tail correlates with the tail's function in salamanders (Mueller *et al.*, 2004). For example, salamanders that have tails that serve an important function in locomotion (e.g. swimming) are less likely to have the ability to drop their tail (Mueller *et al.*, 2004). Although, across other taxa, the functional value of the autotomizable appendage does not always predict the ease of autotomy (Arnold, 1984; Zani, 1996; Fleming *et al.*, 2013). In addition to these two factors, secondary loss of autotomizable body parts has been hypothesized to correlate negatively with other anti-predatory traits (Arnold, 1984; Bateman & Fleming, 2008), such as the ability to fight back actively against a predator (Fleming *et al.*, 2013), and a decrease in predatory pressure (Arnold, 1984; Pafilis *et al.*, 2009).

The evolutionary origins of autotomy are unknown and have received relatively little attention. Hypothetically, there are at least two possible evolutionary routes to sacrificing a body part to escape predation. First, the 'intermediate step' hypothesis proposes that autotomy first arose to reduce the cost of an injured limb or body part, and was then co-opted to escape predation (McVean, 1982; Wasson, Lyon, & Knope, 2002). This hypothesis predicts that when autotomy first arose it took a long time for appendage loss to occur, but organisms maintained this trait because autotomizing a body part slowly came with benefits (e.g. reducing the cost of injury, escaping non-predatory entrapment). Once organisms had the ability to drop a body part, selection could then act on the speed at which the body part was dropped, which, under this hypothesis, eventually led to organisms being able to drop their body parts quickly enough to escape the grasp of a predator. A natural alternative to this hypothesis is one in which autotomizing a limb quickly enough to escape predation evolves without an intermediate-latency step. We refer to this as the 'fast latency' hypothesis. Under this hypothesis, organisms first evolve an anti-predatory trait that deflects attacks towards a specific portion of the body (e.g. false heads, brightly-coloured tails) or they simply have an appendage that is disproportionately attacked. Selection could then drive such an appendage to be removed with ease (i.e. easy to fracture, but the fracturing would not be under the control of the individual), eventually resulting in the organisms being able to drop their own appendage in a rapid manner (i.e. individual control of removing the appendage). Both hypotheses largely overlook the morphological component of autotomy – the fracture plane – and future work on the evolution of autotomy should consider this component as well.

(2) Elaboration of autotomizable appendages

Once an organism has evolved the ability to drop a body part, selection may act on the appendage to increase the efficacy (i.e. increase its benefit) or efficiency (i.e. mitigate its cost) of autotomy. This selection could explain why some autotomizable body parts are so elaborate. Elaboration

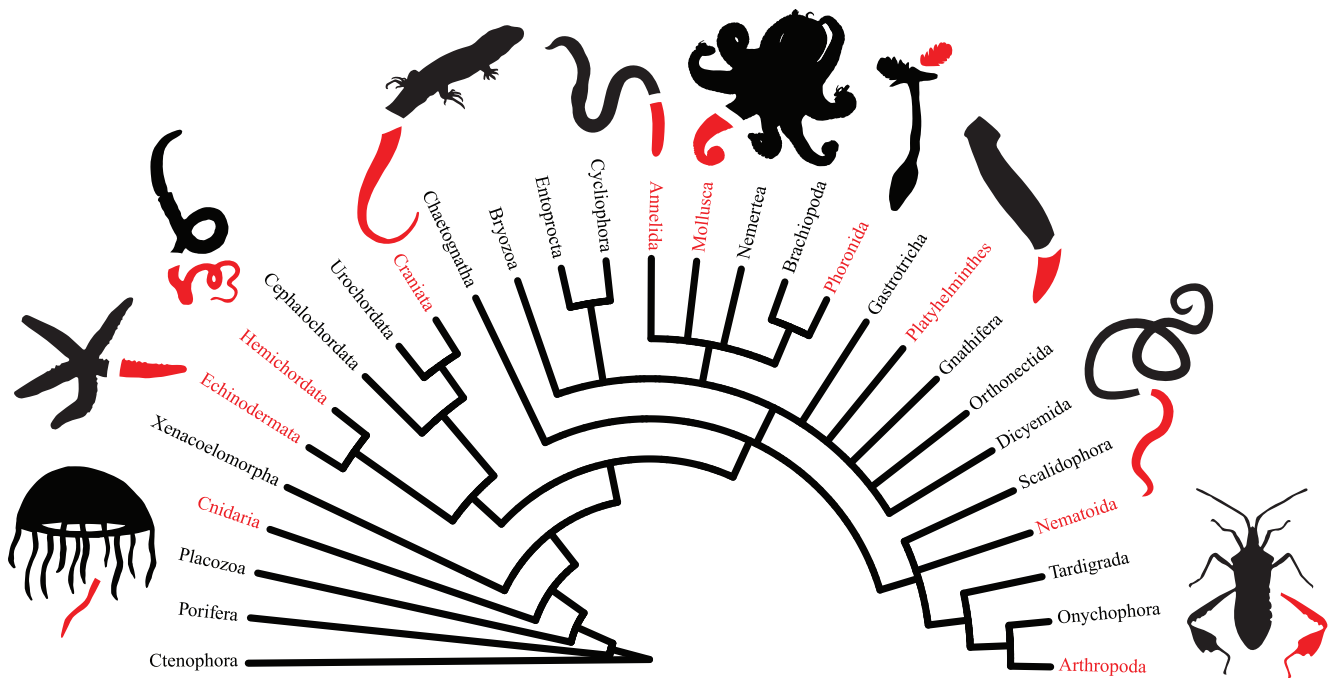


Fig. 1. Autotomy has evolved multiple times throughout Animalia. Stochastic character simulations conducted for this review revealed that autotomy has at least nine independent origins (see Appendix S1 and Fig. S1). Each lineage shown in red on this phylogenetic tree, which is modified from Dunn *et al.* (2014), has at least one species that can induce autotomy. Silhouette images, modified from www.phylopic.org, are visual aids for selected organisms that autotomize, as well as their autotomizable appendages. Silhouette images are not to scale.

of autotomizable appendages includes bright colouration (Fig. 2A; Arnold, 1984), elongation (Fig. 2B; Fleming *et al.*, 2013; Barr *et al.*, 2018), and post-autotomy appendage movement (Dial & Fitzpatrick, 1983). Understanding the evolutionary pressures that promote and constrain these patterns of elaboration remains an exciting avenue of research.

One well-studied example of autotomy efficacy is the bright colouration of some lizard tails (Clark & Hall, 1970; Arnold, 1984; Castilla *et al.*, 1999; Hawlena *et al.*, 2006; Watson *et al.*, 2012) – an appendage that can be regenerated. Such conspicuous colouration has been shown to divert predator attacks towards the autotomizable body part (Clark & Hall, 1970; Cooper & Vitt, 1985; Watson *et al.*, 2012; Bateman, Fleming, & Rolek, 2014; Fresnillo, Belliure, & Cuervo, 2015), which likely increases an individual's ability to survive a predation event. In some cases, however, this bright colouration also increases detection by predators (Bateman *et al.*, 2014; Fresnillo *et al.*, 2015; Nasri *et al.*, 2018, but see Watson *et al.*, 2012), making them risky decoys. Traits that help misdirect attacks towards autotomizable body parts can also be behavioural. Salamanders (Ducey, Brodie, & Baness, 1993) (which can regenerate), lizards (Minton, 1966; Congdon, Vitt, & King, 1974; Arnold, 1984; Mori, 1990) (which can regenerate), and true bugs (Emberts, St. Mary, & Miller, 2016) (which cannot regenerate) have all been observed waving their autotomizable body parts when predators are near. When individuals perform this behaviour,

predators are more likely to strike their autotomizable body part (Ducey *et al.*, 1993; Telemeco, Baird, & Shine, 2011). Thus, predator deflection is one factor likely promoting and/or maintaining the elaboration of autotomizable body parts.

After being autotomized, some body parts will move in a wiggling, thrashing, or violently twitching fashion. This trait increases predator distraction time, ultimately increasing the efficacy of autotomy by providing the individual that autotomized the appendage with more time to escape (Dial & Fitzpatrick, 1983). Post-autotomy appendage movement has evolved independently multiple times (Appendix S1) and is observed in lizards (Higham & Russell, 2010), salamanders (Labanick, 1984), and arachnids [harvestmen (Miller, 1977; Roth & Roth, 1984), spiders (Johnson & Jakob, 1999) and scorpions (Mattoni *et al.*, 2015); of which some can regenerate and others cannot]. In some species, there is also inter-population variation in the vigour of post-autotomy appendage movement, which correlates with local predatory pressure (Cooper, Pérez-Mellado, & Vitt, 2004; suggested in Cromie & Chapple, 2012; Otaibi, Johnson, & Cosentino, 2017). However, in other species, the duration of post-autotomy body-part movement is highly conserved (Pafilis, Valakos, & Fougopoulos, 2005; Pafilis, Pérez-Mellado, & Valakos, 2008; Pafilis *et al.*, 2009). Therefore, the role that current predatory pressure has in maintaining the intensity and duration of post-autotomy body-part movement remains unclear. Nonetheless, there

(A)



(B)



Fig. 2. Autotomizable appendages are often elaborate such as the brightly coloured tail of *Morethia ruficauda* (A) or the elongated tail of *Lialis burtonis* (B). Yet, much remains unknown about the evolution of these autotomizable appendages. Photograph credit: Damian Lettoof.

is still strong evidence to suggest that the movement of autotomizable body parts has been maintained due to its ability to distract predators.

In addition to traits that can increase the success of autotomy, there are also traits that can help mitigate the costs. For example, lizards (Etheridge, 1967; Haacke, 1975, 1976) (which can regenerate), squid (Bush, 2012) (which can regenerate), and scorpions (Mattoni *et al.*, 2015) (which cannot regenerate) have evolved multiple autotomy fracture planes. Having multiple fracture planes along an autotomizable body part allows individuals to minimize the amount of body part that is sacrificed during autotomy: this is referred to as the economy of autotomy (Arnold, 1984). Losing a smaller portion of the body part decreases both the short-term and long-term costs associated with appendage loss (e.g. reduced costs associated with regenerating a smaller appendage; Cromie & Chapple, 2013). However, losing a smaller portion of the body part may also decrease the efficacy of autotomy. Shorter autotomized tail segments, for example, have reduced post-autotomy movement [e.g. distance moved (Cooper & Smith, 2009)], which may decrease the amount of time that an autotomized body part can distract a predator. Although, to date, there is no evidence to suggest that the amount of tail autotomized by lizards influences an individual's probability of survival (Cromie & Chapple, 2013). The number of autotomy fracture planes in a lizard tail also varies both within and across species (Haacke, 1975, 1976; Winchester & Bellairs, 1977; Arnold, 1984; Gilbert, Payne, & Vickaryous, 2013; LeBlanc *et al.*, 2018), and much of the variability within species has been attributed to ontogeny, with age decreasing the number of fracture planes that an individual has (Arnold, 1984). Across-species variability, however, has received far less attention, despite being an ideal topic to understand the role that current and historical pressures have had in influencing autotomizable body parts. For example, as lizard tails become relatively longer/larger they should cost more to regenerate (Bateman & Fleming, 2009), thus, future studies should investigate

whether obligatory regenerative costs associated with tail autotomy can explain variation in the number of fracture planes across species.

The patterns of body-part elaboration above suggest that the ability to drop an appendage may be a key innovation, facilitating trait diversification associated with that body part. Here, we postulate that autotomy facilitates the evolution of colouration, morphological shape elaboration, and behaviour. Phylogenetic comparative analyses in lizards, for example, have found that the ability to autotomize tails evolved before tail colouration (Murali, Merilaita, & Kodandaramaiah, 2018). This suggests that the ability to autotomize promotes the elaboration of the autotomy-related phenotypes, in this case conspicuous tail colouration (Murali *et al.*, 2018). However, the possibility of the opposite evolutionary pathway – that body-part elaboration promotes the evolution of autotomy – cannot be excluded. It should also be emphasized that non-adaptive hypotheses cannot be excluded either. Future studies should explore these avenues more thoroughly.

IV. VARIATION IN THE COSTS AND BENEFITS OF AUTOTOMY

(1) Benefits of autotomy

'Autotomy', as used by Fredericq (1883), attempts to describe the phenomenon in which some animals quickly drop part of their body in a defensive, anti-predatory, manner. However, since then we have gained a better understanding of self-induced appendage loss. For example, we now know that autotomy has additional benefits beyond that of escaping predation (Fig. 3; Maginnis, 2008; Emberts *et al.*, 2017). To understand how autotomy is selected for and maintained throughout Animalia we need a thorough understanding of all the benefits of autotomy. For this review, we place the benefits of autotomy into four broad categories: (i) escaping

predation; (ii) escaping non-predatory entrapment; (iii) reducing the cost of injury; and (iv) increasing reproductive success. It is important to note that these benefits are not mutually exclusive and that selection may be maintaining autotomy within a population due to any combination of these categories.

Escaping predation is the most investigated benefit of autotomy. Several studies have shown that individuals are more vulnerable to predation once they have dropped their autotomizable body part (e.g. Congdon *et al.*, 1974; Stoks, 1998; Downes & Shine, 2001; Bateman & Fleming, 2006*a*). This result is likely to be due to several factors. Most notably, individuals without their autotomizable body part cannot re-autotomize that appendage as a last-ditch effort to escape predation. This is particularly relevant for animals that do not regenerate appendages. However, the observed differences in vulnerability could also be due to predators differentially attacking individuals that are missing their autotomizable appendage (i.e. predator preference, but see Congdon *et al.*, 1974; Lancaster & Wise, 1996; Stoks, 1998). Moreover, individuals missing body parts often have reduced locomotor capabilities (Fleming & Bateman, 2007; Maginnis, 2006; Fleming *et al.*, 2007; but see Lu *et al.*, 2010), which would inhibit their ability to flee. No study has teased these factors apart. To date, the degree to which autotomy itself increases an individual's probability of escaping a predation event has yet to be demonstrated. Such a study would require manipulating an individual's ability to autotomize without removing the autotomizable body part and then comparing differences in escape ability between those that can autotomize and those that cannot, ideally using natural predators. Despite the lack of direct, experimental studies, there is still strong evidence to suggest that autotomy has an anti-predatory benefit.

Other evidence for autotomy having an anti-predatory benefit includes anecdotal observations, the speed at which autotomy is induced, and correlations between autotomy and local predation pressure. Autotomy of a body part during a predation event has been observed in numerous taxa [e.g. lizards (Congdon *et al.*, 1974); spiders (Punzo, 1997); crustaceans (Lawton, 1989; Wasson *et al.*, 2002); earthworms (Sugiura, 2010); salamanders (Labanick, 1984)] and the most parsimonious explanation is that autotomy occurs to escape predation. Additionally, the speed at which organisms autotomize a body part has been used, implicitly, as evidence for an anti-predatory benefit. This can be seen in studies where researchers terminate autotomy trials after 10–120 s (Easton, 1972; Cooper *et al.*, 2004) if autotomy has yet to occur. Presumably these time points were selected because predation events often occur rapidly, and being unable to autotomize quickly suggests that autotomy would fail to serve as an escape mechanism. Correlations between predation pressure and the latency or frequency to autotomize across populations also suggest that autotomy in such taxa is primarily used to escape a predation event (e.g. Pafilis *et al.*, 2009; Brock *et al.*, 2015). On the other hand, lack of such correlations suggests that autotomy is not exclusively used

to escape predation. On some predator-free islands, for example, gecko populations have higher rates of autotomy than in mainland populations, which suggests that autotomy functions in other contexts, in this case, to reduce the cost of injury from intraspecific competition (Itescu *et al.*, 2017).

Traits associated with escaping are often associated with escaping predation, but there are also scenarios in which autotomy would benefit individuals that need to escape from non-predatory entrapment (e.g. Maginnis, 2008; Hodgkin, Clark, & Gravato-Nobre, 2014). Within arthropods, non-predatory entrapment often manifests itself in the form of a bad moult. All arthropods go through multiple moulting episodes during development, and in some cases throughout adult life. During this process, limbs can become stuck (Fig. 3B). To avoid entrapment and potential death, individuals may simply autotomize these limbs. Autotomy to escape a bad moult has been observed in coreids (Emberts *et al.*, 2016), walking sticks (Maginnis, 2008), spiders (Foelix, 1996), and decapods (Wood & Wood, 1932). In some cases, evading entrapment requires autotomizing several limbs. The crab *Carcinus maenas*, for example, has been observed autotomizing up to three legs to escape a fouled moult (Wood & Wood, 1932). Another non-predatory entrapment scenario can include getting stuck in tree sap/resin (hypothesized in Maginnis, 2008), although in certain contexts this may be considered predatory entrapment as well [e.g. arthropods caught by carnivorous sundews (Cross & Bateman, 2018)].

Autotomy can also be used to reduce the cost of (externally induced) injury, which can occur from predatory encounters or intraspecific competition. Possessing an injured limb makes an individual susceptible to blood loss and infection, as does autotomy (Slos, De Block, & Stoks, 2009; Yang *et al.*, 2018). However, in terms of survival, injury is more costly than autotomy (Emberts *et al.*, 2017; Yang *et al.*, 2018). This cost differential makes it possible for individuals to gain a survival benefit by autotomizing their injured body parts, and experimental manipulations have found support for this hypothesis (Emberts *et al.*, 2017). The survival difference that comes with autotomizing injured body parts at a predetermined breakage plane is likely due to (i) a reduction in the amount of blood that is lost, and/or (ii) having a less-compromised immune system. Previous research has found support for both these mechanisms: blood loss following autotomy is negligible (Wake & Dresner, 1967; Foelix, 1996; Lesiuk & Drewes, 1999; Wilkie, 2001) and the immune system of recently autotomized individuals is less compromised than those that have been injured (Yang *et al.*, 2018). Envenomation is another source of injury, during which the predator punctures the outer layer of its prey and injects it with a toxin to debilitate or kill. If envenomation occurs on an autotomizable body part, individuals of several taxa have been observed autotomizing these compromised appendages, resulting in their survival [crabs (Muscatine & Lenhoff, 1974); spiders (Eisner & Camazine, 1983); grasshoppers (Ortego & Bowers, 1996)]. In addition to the survival benefit that comes with autotomizing injured body parts,

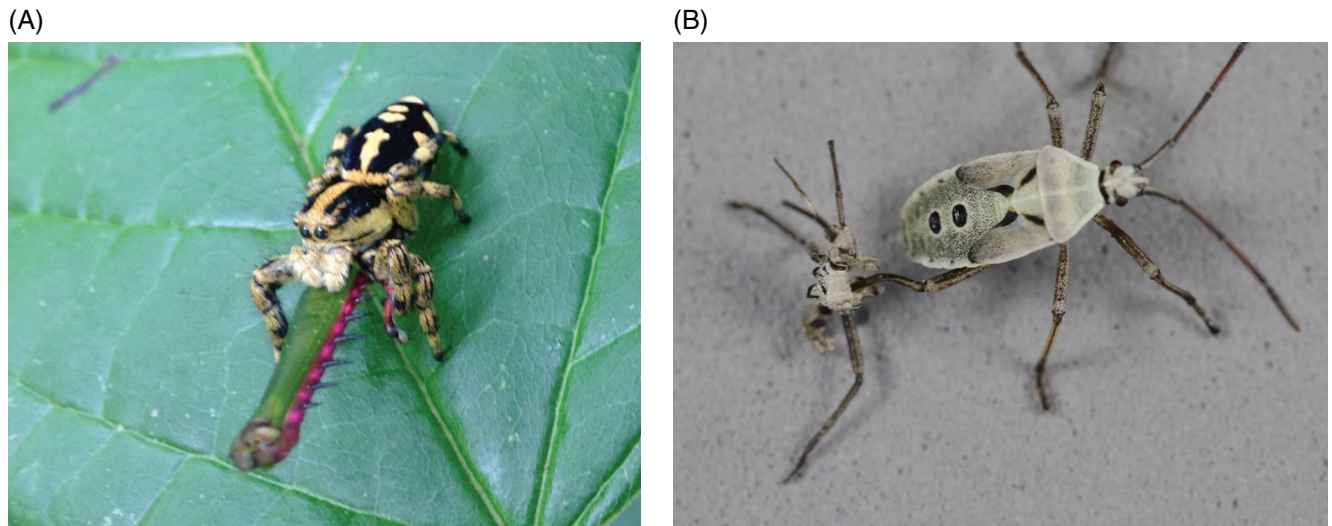


Fig. 3. There are multiple benefits associated with autotomy. Survival benefits include escaping predation, escaping non-predatory entrapment, and reducing the cost of injury. (A) A jumping spider holding the autotomized limb of an orthopteran. Photograph credit: Ummat Somjee. (B) A coreid entrapped in its previous moult. Photograph credit: Zachary Emberts.

there may be other benefits. For example, autotomy of injured body parts may reduce the metabolic cost of possessing a non-functional appendage. The number and diversity of organisms that have been observed autotomizing an injured body part suggests that this is a widespread benefit [e.g. lizards (Elwood, Pelsinski, & Bateman, 2012), sea stars (Glynn, 1982; Bingham, Burr, & Head, 2000; Ramsay *et al.*, 2001), true bugs (Emberts *et al.*, 2017) and crabs (McVean, 1975)].

Autotomy can also be used to increase an individual's reproductive success. In several species of arachnids, for example, males will autotomize their intromittent organs inside a female's reproductive tract (Fromhage & Schneider, 2006; Uhl *et al.*, 2010). These intromittent organs are not regenerated, but such genital mutilation is generally considered to be advantageous in these species because of low female encounter rates (Uhl *et al.*, 2010). In some cases, the autotomized limb functions as a copulatory plug, temporarily preventing other males from mating with the female. In other cases, the autotomized structure plugs the female's sperm storage site (Berendonck & Greven, 2000; Snow *et al.*, 2006). In either case, successfully plugging the reproductive tract can increase a male's fertilization success (Snow *et al.*, 2006). Autotomy can also be used as a component of nuptial gifts (Ghislandi *et al.*, 2015). In *Pisaura mirabilis*, a nuptial-gift-giving spider, males have been observed autotomizing their limbs and including them in their nuptial gifts, making the gifts larger (Ghislandi *et al.*, 2015). Males that provide females with larger gifts mate for a longer duration and have higher fertilization success (Stalhandske, 2001). Since autotomy can be costly, especially in the case of autotomizing intromittent organs (i.e. complete loss may result in the male becoming functionally sterile, but see Snow *et al.*, 2006), future studies should investigate the scenarios in which individuals decide to autotomize their limbs in these mating contexts.

Given that autotomy has multiple benefits, it is important that we avoid the assumption that anti-predation is the sole, or even the primary, benefit of autotomy. Future studies should explicitly test for, and, ideally, characterize which benefits apply to specific species. Moreover, should autotomy be beneficial in multiple contexts, studies should seek to approximate the ecological relevance of each benefit. In so doing, we would gain a better understanding of how autotomy is selected for and maintained within populations. One way to test amongst different autotomy benefits is through predator exclusion. Using this method Maginnis (2008) found that approximately 50% of total limbs lost in the stick insect *Didymuria violescens* was not due to predation, and postulates that these limbs were autotomized to escape non-predatory entrapment.

(2) Costs of autotomy

The idea that losing body parts comes with negative consequences is intuitive and has been widely studied (reviewed in Maginnis, 2006; Fleming *et al.*, 2007). One reason that the negative consequences of autotomy have been so well studied is simply logistical feasibility. Researchers can control for aspects such as the time since autotomy, the conditions under which appendage loss occurred, and the force applied to release the limb. Despite being well studied, more recent research on the costs of autotomy has increased the resolution, explanatory power, and implications of these consequences. For example, studies have begun to follow autotomized individuals for longer periods of time, which has allowed researchers to investigate whether the costs of autotomy are mitigated (e.g. *via* regeneration or muscular compensation) or maintained over time (e.g. Lin *et al.*, 2017). Since the costs of autotomy and regeneration have been thoroughly reviewed previously (Maginnis, 2006; Fleming

et al., 2007; Bateman & Fleming, 2009; Higham *et al.*, 2013), we aim here to build upon these previous reviews by summarizing new findings and novel approaches to studying the negative consequences of autotomy.

Fundamentally, fitness costs of autotomy can be seen as either direct costs to survival or direct costs to reproduction. Even though these categories can overlap or be correlated, we use them here to convey efficiently the new available information. Below we discuss how more proximate costs contribute to these categories.

Costs of autotomy on locomotion have been studied extensively. Leg and tail loss have been shown to reduce the locomotor performance (including velocity, acceleration, and endurance), as well as stability and control (manoeuvrability) of an animal running, jumping, flying or swimming (reviewed in Maginnis, 2006; Fleming *et al.*, 2007). This reduction in locomotion can compromise the chances of successfully escaping a future encounter with a predator, which indirectly compromises survival, as well as other life-history traits, such as foraging and reproduction. Recent research has built upon these findings by investigating the kinematic and morphological mechanisms that decrease locomotor performance after autotomy. For instance, Jagnandan & Higham (2017) experimentally demonstrated that changes in the locomotion of lizards after tail loss were due to the absence of lateral undulations of the tail, rather than the loss of body mass *per se* or the anterior shift in the centre of mass. Additionally, in *Anolis carolinensis*, tail autotomy affected their in-air stability while jumping (Gillis, Bonvini, & Irschick, 2009). Context- and substrate-dependent effects of autotomy on locomotion have also been demonstrated. Examples include the width of the surface on which *A. carolinensis* could run (Hsieh, 2016), the degree of surface incline while moving in cellar spiders *Pholcus manueli* (Gerald *et al.*, 2017) and fiddler crabs *Uca pugilator* (Gerald & Thiesen, 2014), as well as the three-dimensional substrate complexity which affects movement in the harvestman taxa *Leiobunum* (Houghton, Townsend, & Proud, 2011), *Holmbergiana weyemberghi* (Escalante, Albín, & Aisenberg, 2013), and *Prionostemma* (Domínguez *et al.*, 2016). Lastly, some studies have included the long-term monitoring of animals post-autotomy. Testing locomotor performance repeatedly has allowed us to ask questions about potential recovery from autotomy, as well as the influence of regeneration. For instance, limb kinematics and ground reaction forces changed immediately after tail autotomy in the leopard gecko (*Eublepharis macularius*), but these geckos recovered to initial pre-autotomy levels over the course of 22 weeks (Jagnandan, Russell, & Higham, 2014) as the tail was regenerated. A similar pattern of recovery after regeneration was observed in the lacertid lizard *Psammodromus algirus* (Zamora-Camacho *et al.*, 2016). In *Anolis carolinensis* some individuals recovered initial in-air stability over the course of 5 weeks post tail autotomy (Kuo, Gillis, & Irschick, 2012). Finally, *Prionostemma* harvestmen recovered pre-autotomy locomotor performance in a much shorter time frame of 24 h (I. Escalante, unpublished data). This latter example highlights the ways

animals can recover locomotor performance in the absence of regeneration, mostly by modifying kinematic features of movement.

Recent work has also studied the costs of autotomy on physiology and the energetics of locomotion, with some studies showing costs and others finding no costs. For example, autotomy was associated with short-term changes in cardiac output in blue crabs *Callinectes sapidus* (McGaw, 2006), an increase in the metabolic costs of locomotion (CO₂ emissions) in crickets *Gryllus bimaculatus* (Fleming & Bateman, 2007), and an increase in standard metabolic rate in lizards *Liolaemus belli* (Naya *et al.*, 2007). Some studies, however, have found no costs of autotomy on resting metabolic rates. For instance, Fleming *et al.* (2009) found lower CO₂ production during exercise by geckos (*Lygodactylus capensis*) after autotomy, which was potentially associated with the loss of tissue. Starostová, Gvoždík, & Kratochvíl (2017) found no differences in the resting metabolic rates of intact and autotomized geckos (*Paroedura picta*) immediately after autotomy or over the 22-week regeneration period. Additionally, the temperature regulation of lizards (*Psammodromus algirus*) did not change after tail autotomy (Zamora-Camacho, Reguera, & Moreno-Rueda, 2015). One additional physiological approach to quantifying the costs of autotomy involves metabolites, and cellular and histological processes. For instance, biochemical changes at the cellular level were studied in the Chinese mitten crab (*Eriocheir sinensis*), where Yang *et al.* (2018) found an increase in the concentration of several metabolic compounds after induced cheliped autotomy. This was suggested to be an efficient response to trauma when compared to regular ablation, as autotomized individuals recovered initial levels earlier than ablated individuals (Yang *et al.*, 2018). Regeneration after autotomy also has costs (Maginnis, 2006). In lizards, regenerated tails have different lipid and protein content, as well as greater amounts of skeleton and muscle, than original tails (Boozalis, LaSalle, & Davis, 2012; Russell *et al.*, 2015). This redistribution of resources, particularly protein, has been shown to affect the digestive performance (gut passage time) in *Podarcis erhardii* lizards (Sagonas *et al.*, 2017), and shell growth in *Satsuma caliginosa* land snails (Hoso, 2012). Finally, the nervous system and associated histological mechanics of regeneration after autotomy were recently investigated in *Coscinasterias muricata* sea stars (Byrne *et al.*, 2019). The authors showed that glia-like cells and the rapid arrival of migratory cells through haemal and coelomic compartments suggest that the autotomy plane is adapted to promote wound healing and regeneration (Byrne *et al.*, 2019). These studies used careful experimental designs to control for the potential confounding factors of stress and injury. Nonetheless, we consider it imperative that future research explicitly aims to tease apart the actual effect of autotomy or regeneration, rather than the injury, recovery, experience or even compensation, on these physiological and biochemical proxies.

A novel approach to the costs of autotomy has been studying its effect on disease and parasite loads. For instance,

a reduced immune response and antioxidant defences were recorded in *Lestes viridis* damselfly larvae after lamellae autotomy, an appendage used for locomotion and breathing (Slos *et al.*, 2009). Additionally, increased mortality attributed to parasitoids after autotomy was found in two *Parapodisima* grasshopper species (Miura & Ohsaki, 2015). In three species of *Sceloporus* lizards, individuals with a regenerated tail had higher ectoparasite loads than did intact individuals (Argaez, Solano-Zavaleta, & Zúñiga-Vega, 2018), although it is challenging to tease apart the effects of autotomy from regeneration in this case.

Another new focus has been correlating autotomy with behavioural syndromes (or personalities), as well as with potential compensatory strategies. For example, in Cuban anole lizards (*Anolis sagrei*), individuals with a higher tendency to explore ('bold') were more likely to autotomize their tail than 'shy' individuals (Kuo, Irschick, & Lailvaux, 2015). A similar pattern was found in damselfly larvae of *Ischnura pumilio*, in which individuals with increased risk-taking behaviour also had a higher probability of autotomizing their caudal lamellae (Delnat, Debecker, & Stoks, 2017). These findings support the hypothesis that animals rely on autotomy as a defence at the individual level with much context-based variation. Additionally, these findings suggest ways that animals may incorporate a cost/benefit when deciding to induce autotomy.

Long-term and interdisciplinary approaches to studying autotomy are also emerging. For instance, a seven-year long mark–recapture study coupled with statistical modelling quantified the costs of autotomy on survival in a lizard (*Takydromus viridipunctatus*) population. Because of the study's design, these predatory pressures could be attributed to specific bird species (Lin *et al.*, 2017). These new results provide a compelling and complete multi-component approach to understanding the costs of autotomy.

Fewer studies have explored the direct costs of autotomy on reproduction than on survival. However, recently, important contributions have been made in understanding how autotomy affects several traits and stages associated with animal reproduction. Regarding initial stages, male fiddler crabs (*Uca mjoebergi*) that fully regenerated their major claw after autotomy were less likely to hold and defend territories than intact individuals (Reaney *et al.*, 2008). Moreover, autotomy, with or without regeneration, has repeatedly been found to decrease an individual's probability of winning intraspecific fights in the context of reproduction (Smith, 1992; Martín & Salvador, 1993; Abello *et al.*, 1994; Reaney *et al.*, 2008; Daleo *et al.*, 2009; Wada, 2016; Yasuda & Koga, 2016; Emberts *et al.*, 2018). In many cases these autotomizable appendages are used directly during intraspecific interactions (e.g. a crab's claw) so the loss of the appendage comes with direct costs (Abello *et al.*, 1994). However, in other cases, the autotomizable appendage is not directly involved in agonistic interactions (e.g. a lizard's tail), but its absence still decreases the individual's probability of winning (Martín & Salvador, 1993). These patterns could be due to other marginal costs associated with losing an

appendage, such as reduced locomotive ability and/or higher predatory risk aversion, which could be enough to result in a decrease in fighting ability. Alternatively, if size is used to assess fighting ability and the presence of the autotomizable appendage makes an individual appear larger, autotomy may compromise social/fighting status (Fox, Heger, & Delay, 1990).

In addition to these fighting costs, autotomy has been shown to influence courting and mating behaviour. Behavioural compensation in courting effort post-autotomy has been recorded in male *Dianemobius nigrofasciatus* crickets, which increase their calling behaviour after limb autotomy (Matsuoka, Miyakawa, & Ishihara, 2011). On the other hand, the loss of even one of the two pedipalps (appendages used for courtship and sperm transfer) in males reduced the intensity of courtship of the wolf spider *Pardosa milvina* (Lynam, Owens, & Persons, 2006). Limb-autotomized male *Menochilus sexmaculatus* ladybird beetles experienced a delayed mating start and duration (Shandilya, Mishra & Omkar, 2018). Moreover, mating success was found to be lower in autotomized males of the wolf spider *Schizocosa ocreata* (Taylor *et al.*, 2008), as well as in the cactus bug *Narnia femorata* (Emberts *et al.*, 2018). In the cricket *Gryllus bimaculatus* experimental pairings when the female was missing either a middle or hind leg were less likely to transfer sperm (Bateman & Fleming, 2006b). This was likely due to the inability of the female to mount the male properly.

In terms of fecundity and offspring survival, few studies have been able to provide evidence of the effects of autotomy. In the ladybird beetle *Menochilus sexmaculatus*, egg sacs fertilized by limb-autotomized males had lower fecundity and a smaller per cent of egg viability than those fertilized by intact individuals (Shandilya *et al.*, 2018). Whether this pattern is mediated by female choice or is a byproduct of male condition is unknown, making this a topic that deserves further investigation. On the other hand, males that autotomized as juveniles (without the ability to regenerate) produced more offspring than intact males in the cactus bug *N. femorata* (Joseph *et al.*, 2018).

Overall, recent findings indicate that autotomy can have direct costs on one or more stages of animal reproduction. The absence of an effect on a single trait or stage does not necessarily indicate that reproduction is unaffected in that species. Consequently, we urge researchers to cover more than one stage in each taxon (i.e. access to mates, courtship, mating, and fecundity) to better understand if missing body parts compromises any measure of fitness.

V. ECONOMIC THEORY OF AUTOTOMY: PREDICTING WHEN AN INDIVIDUAL SHOULD AUTOTOMIZE

Theoretical investigations of the decisions individuals make to escape a potentially harmful interaction are common. However, most of this work investigates flight initiation distance (FID) in response to an approaching predator

(Ydenberg & Dill, 1986; Cooper & Frederick, 2007, 2010) and few theoretical studies consider autotomy, despite previous calls for action (Juanes & Smith, 1995). Theoretical models, even heuristic ones, are useful because they allow us to generate specific predictions and require us to dictate specific underlying assumptions, which provides directions for future empirical work.

Here, we modify the economic theory of escape to generate an economic theory of autotomy. In ‘the economics of fleeing from predators’, Ydenberg & Dill (1986) develop two hypotheses governing when an individual should flee. The first is based purely on detection of a predator, and predicts that an individual flees as soon as the predator is detected, whereas the second hypothesis is one of choice: given that the individual detects the predator it then chooses whether it should stay or flee. Modified for an autotomy framework, the first hypothesis would predict that individuals initiate autotomy as soon as they are entrapped. The second hypothesis is still one of choice; given that the individual is entrapped it then chooses whether to struggle (e.g. kick, fight back, release chemical defences) or autotomize to escape (discussed in Wasson & Lyon, 2005). For both hypotheses we can generate predictions about when an individual should autotomize.

The first hypothesis predicts that individuals should initiate autotomy as quickly as they can. Therefore, any differences in the latency to autotomize should be explained by differences in the amount of time it takes an individual to physically perform autotomy. Factors that contribute to an individual’s ability to perform autotomy include: (i) the amount of force required to break an autotomy fracture plane, and (ii) the amount of time it takes an individual to generate that amount of force. Thus, this hypothesis can be considered one of morphological and physiological constraints. Previous studies have investigated the amount of force it takes to break an autotomy fracture plane in both vertebrates [lizards (Fox, Perea-Fox, & Franco, 1994; Fox, Conder, & Smith, 1998)] and invertebrates [damselflies (Gleason, Fudge, & Robinson, 2014), starfish (Marrs *et al.*, 2000), crabs (Prestholdt *et al.*, 2018)]. However, these studies often fail to identify the amount of time it takes an organism to generate the same amount of force and assume that the amount of force required to perform autotomy positively correlates with the latency to autotomize. Future work should test this assumption.

It is important to note that the no-choice hypothesis does not take context into consideration. Consequently, this hypothesis predicts that an individual should autotomize a limb entrapped by a predator just as quickly as a limb stuck in tree sap. Morphology and physiology certainly contribute to the amount of time it takes an individual to autotomize a limb; however, what differentiates the no-choice hypothesis from the behavioural-choice hypothesis is that the latter predicts that behaviour contributes to most of the variation in the latency to autotomize. Under the behavioural-choice hypothesis, context matters. For example, how important is the limb to an individual’s future reproductive success and survival, will the limb be regenerated, and how dangerous

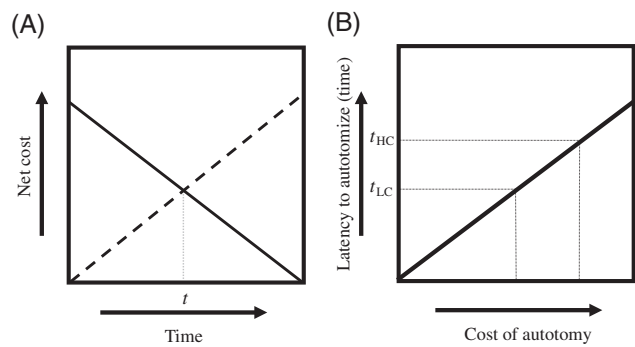


Fig. 4. Under the economic theory of autotomy (A), an individual should perform the action that is the least costly. The dashed line represents the net cost of retaining a compromised limb over time, whereas the solid line represents the net cost of autotomizing a compromised limb over time. An individual should refrain from autotomizing if the cost of autotomy is greater than the cost of retaining the compromised limb (time $< t$). However, once the cost of autotomy is less than the cost of retaining a compromised limb (time $> t$), then the individual should readily autotomize. (B) This model predicts that there should be a positive correlation between the cost of autotomy and the latency to autotomize, if the benefits of autotomy are held constant. t_{LC} is the predicted latency to autotomize when autotomy costs are low; t_{HC} is the predicted latency to autotomize when autotomy costs are high. Note that when it is more costly to autotomize, an organism should wait longer before dropping their appendage.

is the current situation (e.g. entrapped in tree sap *versus* a predator)?

Through an economic lens, determining when an individual should behaviourally autotomize simply becomes a cost/benefit analysis. That is to say, at any given moment (in this case, time, t ; Fig. 4) an individual should perform the action that is the least costly. Therefore, an individual should not autotomize if the cost of autotomy is greater than the cost of retaining the compromised limb (Fig. 4; time $< t$). However, once the cost of autotomy is less than the cost of retaining a compromised limb (Fig. 4A; time $> t$), then the individual should readily autotomize. Consequently, this economic model predicts that the latency to autotomize is positively correlated with the cost of autotomy (given that the benefits are the same; Fig. 1B), which formalizes multiple hypotheses found throughout the autotomy literature (Wood & Wood, 1932; Robinson, Abele, & Robinson, 1970; Arnold, 1984; Fox *et al.*, 1998; Guffey, 1998; Pears, Emberts, & Bateman, 2018). Note that if an organism is capable of regeneration, then the costs of autotomy include the costs and benefits of regeneration. Thus, depending on whether regeneration can reduce the net cost of autotomy or exaggerates the net cost of autotomy (which can potentially occur under obligatory regeneration, as discussed in Maginnis, 2006) this economic model would predict the organism to autotomize more quickly or more slowly, respectively.

A key assumption of this economic model is that the probability of successfully using autotomy decreases with time (Fig. 4). For example, we assume that an individual who autotomizes their limb within 1 s has a better probability of surviving a predation event than an individual who waits 60 s. Although we believe this to be a safe assumption, the shape of the relationship between latency to autotomize and the probability of successfully using autotomy remains unclear (e.g. linear, decelerating power, accelerating power, or logistic). Another assumption of this economic model is that all individuals perceive that their limb is compromised (e.g. entrapped, injured) instantaneously. Future research should investigate the validity of these assumptions. We also encourage others to develop and expand upon this and/or other autotomy models to help us understand what drives behavioural variation in the latency to autotomize both within and among species.

VI. IMPLICATIONS OF AUTOTOMY ON ORGANISMAL AND ENVIRONMENTAL INTERACTIONS

(1) Predator–prey interactions

When autotomy is used in an anti-predatory context, it influences the current predator–prey interaction. Most notably, once an organism autotomizes, it presents the predator with several new choices. The predator could choose to (i) release the autotomizable body part and continue pursuing the prey, (ii) handle and consume the autotomized body part, then continue pursuing the prey, or (iii) handle and consume the autotomized body part and not continue to pursue the prey. Much remains unknown about these choices because studies often focus on the prey species (e.g. did the prey use autotomy, did autotomy enable escape?). However, a handful of studies have provided some insights into the predator's actions. When investigating the role of post-autotomy appendage movement, Dial & Fitzpatrick (1983) showed that a predatory cat ignored the autotomized tails of *Anolis carolinensis*, but attacked (i.e. handled) the autotomized tails of *Scincella lateralis*. Both species exhibit post-autotomy appendage movement, but the movement exhibited by *S. lateralis* is more vigorous, and ultimately more successful at distracting the predator (Dial & Fitzpatrick, 1983). In predator–prey interactions between different species of crabs, approximately 85% of the crab predators handled and consumed the autotomized claw of their prey instead of continuing pursuit (Wasson *et al.*, 2002). In the remaining 15%, the predator spent time handling the autotomized appendage, but continued pursuit of the prey (Wasson *et al.*, 2002). Moreover, in predation trials between scorpions (predator) and wolf spiders (prey), scorpions will consume autotomized limbs (Punzo, 1997). Consumption of the autotomized appendage is often implicit in autotomy studies (e.g. Congdon *et al.*, 1974), but future studies should explicitly state whether the appendage was consumed and whether the predator continued to pursue

their prey. Future studies should also investigate the factors that contribute to these predator decisions. Some factors that could potentially influence a predator's decision include, the size of the autotomizable appendage (i.e. the meal at hand), the predator's level of hunger, and the distance an organism flees after autotomizing their limb. In addition to autotomy influencing the current predator–prey interaction, the absence of an autotomizable appendage can also influence future predator–prey interactions. For example, individuals without their autotomizable body parts are less successful at escaping predators (e.g. Congdon *et al.*, 1974; Stoks, 1998; Downes & Shine, 2001; Bateman & Fleming, 2006a; as discussed in Section IV.1). However, despite predators being more successful at capturing organisms missing an autotomizable appendage, there is no evidence to suggest that predators differentially pursue such prey (Congdon *et al.*, 1974; Lancaster & Wise, 1996; Stoks, 1998).

Loss of an autotomizable appendage can also affect an individual's foraging behaviour and feeding success (i.e. the influence of autotomy on predator–prey interactions when the organism that autotomizes is also a predator). This has mostly been studied in crustaceans because their autotomizable claws are directly associated with foraging, and these studies have frequently found that the loss of a claw reduces foraging efficiency (Smith & Hines, 1991; Davis *et al.*, 2005; Patterson, Dick, & Elwood, 2009; Flynn *et al.*, 2015, but see Smith & Hines, 1991; de Oliveira, Christofolletti, & Barreto, 2015). Moreover, autotomized crustaceans feed upon smaller and more easily attainable prey (e.g. prey with reduced shell thickness) when compared to intact individuals (Davis *et al.*, 2005; Flynn *et al.*, 2015). These altered foraging patterns also extend beyond crustaceans. Keeled earless lizards, *Holbrookia propinqua*, without their tail decrease their foraging effort (Cooper, 2003), damselfly larvae without their autotomizable tail lamellae are less successful at capturing prey (Stoks, 1998), and wolf spiders missing a leg prey upon smaller organisms (Brueseke *et al.*, 2001). These altered patterns of foraging behaviour and feeding success highlight that autotomy can potentially have a cascading effect on population and community dynamics, but the magnitude of these effects remain largely unquantified. Even less is known about the implications of regeneration on these effects, and future work is merited.

(2) Intraspecific competition

Not only can autotomy result from intraspecific competition (Van Buskirk & Smith, 1991; Juanes & Smith, 1995; Itescu *et al.*, 2017), but the previous loss of an autotomizable appendage can also alter the dynamics of these interactions. Several studies have found that the absence of an autotomizable appendage decreases an individual's probability of winning intraspecific fights (discussed in Section IV.2). Although a decrease in fighting ability after autotomy is clear, there is variation in the degree to which organisms alter their behaviours associated with these interactions. Some studies have found that organisms missing an appendage change their fighting behaviour by (i) avoiding

agonistic interactions, or (ii) altering how they engage in these interactions. In fiddler crabs, for example, males that have autotomized their major claw search for vacant mating burrows instead of fighting for occupied ones (Bookmythe *et al.*, 2010). Moreover, other crustaceans have been observed implementing fighting tactics that conceal the loss of their weapon (O'Neill & Cobb, 1979; Berzins & Caldwell, 1983). However, some studies have found that organisms missing an autotomizable appendage behave in a similar manner to their intact counterparts (Maginnis *et al.*, 2015; Yasuda & Koga, 2016); for example, in the leaf-footed cactus bug *N. femorata*, individuals missing their autotomizable weapons are just as likely to engage in intraspecific interactions as are intact individuals, and weaponless individuals still try to use their weapon, behaving as if the weapon was still present (Emberts *et al.*, 2018). The factors that drive such contrasting responses across species remains unclear.

(3) Movement and habitat selection

Movement and habitat choice can have numerous consequences on population and community dynamics, including foraging and reproduction, and organisms missing an autotomizable appendage often use their habitat differently (e.g. Martín, Salvador, & Martín, 1992; Houghton *et al.*, 2011). Most notably, they are more risk averse in their habitat use. This often manifests itself as a reduction in the amount of time spent in open areas (Martín *et al.*, 1992; Salvador *et al.*, 1995; Stoks, 1999; Downes & Shine, 2001; Cooper, 2003, 2007; Bateman & Fleming, 2006a; Cooper & Wilson, 2010). However, a few studies have found no notable difference in exposure time following autotomy [lizards (McConnachie & Whiting, 2003); crickets (Matsuoka *et al.*, 2011)]. Loss of an autotomizable appendage also appears to decrease overall activity in some species (Salvador *et al.*, 1995; Martín & Salvador, 1997; Downes & Shine, 2001; Cooper, 2007), but other studies have also found that this is not consistent across taxa (Cooper, 2003; McConnachie & Whiting, 2003). This across- and within-species variation in activity levels following autotomy might be explained by context dependency. The absence of an autotomizable appendage – the caudal lamellae – in damselfly larvae, for example, does not influence activity levels when a predator is present, but in the absence of predation individuals that have lost their autotomizable appendage show decreased activity (Stoks, 1998). Loss of an autotomizable tail also decreases home-range size in both the male Iberian rock lizard and the long-tailed lizard (Salvador *et al.*, 1995; Martín & Salvador, 1997), which affects the number and identity of conspecifics that an individual interacts with. Future studies should continue to investigate the effects of autotomy on population and community dynamics, while also considering the implications of regeneration.

VII. APPLICATIONS OF AUTOTOMY RESEARCH

The study of autotomy has provided insights into fishery management, robotics, and conservation biology. Of all the animals that can autotomize, Crustacean autotomy currently has the most commercial applications. To provide one example, approximately 10.5 million stone crabs (*Menippe*) are caught, declawed, and then released in Florida (United States) each year (Muller, Bert, & Gerhart, 2006). Because stone crabs can regenerate their claws (Savage & Sullivan, 1978), this practice has the potential to create a sustainable fishery. However, research has shown that manually removing both claws reduces laboratory survival rates by almost 50% (Davis *et al.*, 1978). Furthermore, inducing claw autotomy, as opposed to manually declawing, reduces stress responses and feeding suppression (Patterson, Dick, & Elwood, 2007). Thus, inducing autotomy of a single claw may be a more sustainable practice. Autotomy has also been considered in robotics as well. For instance, Wilshin *et al.* (2018) studied the postural and kinematic adjustments of wolf spiders after autotomy and outlined how such knowledge could be used to improve robotic design. Moreover, engineers have started incorporating similar biomimetic and bio-inspired designs for limb loss compensation into their research (Cully *et al.*, 2015). In terms of conservation biology, autotomy has the potential to show how animals are affected and respond to environmental change. For example, research on damselfly larvae has explored the effects of pesticides, changing temperatures, and competition on the incidence of autotomy (Janssens, Verberk, & Stoks, 2018; Op de Beeck, Verheyen, & Stoks, 2018). Future studies on autotomy should continue to outline how the work can be translated into other areas of research, particularly those with more direct applications.

VIII. FUTURE DIRECTIONS

Despite being studied for over a century, fundamental questions about autotomy remain unanswered. For example, how does autotomy evolve? Future studies should investigate how populations can go from being unable to drop their appendage to being able to drop their appendage quickly enough to escape the grasp of a predator. One way to approach this is to use phylogenetic comparative methods to estimate the ancestral rate of autotomy at its origins. If the ancestral rate of autotomy is slow it would support the intermediate-step hypothesis, whereas if the rate of autotomy was rapid it would support the fast-latency hypothesis. However, there is currently no evidence to support either hypothesis and these hypotheses largely ignore how the morphological component – the autotomy fracture plane – evolves. We have also provided evidence that post-autotomy appendage movement, a form of autotomizable limb elaboration, has evolved independently multiple times (Appendix S1). Such convergent evolution

suggests that autotomizable limbs are under selection to increase the efficacy or efficiency of autotomy. Thus, it might be most biologically meaningful to investigate the evolution of autotomy and autotomizable limbs simultaneously, which we collectively refer to as the autotomy phenotype.

In addition to questions about evolution, the effects of autotomy on population and community dynamics should also be investigated more explicitly. For example, is a reduction in home-range size a common consequence of autotomy? If so, what is the magnitude of this reduction and what are its repercussions? Future works should also explicitly investigate how autotomy influences predator–prey interactions, specifically when the organism that autotomizes is also a predator. We noted that appendage loss influences an organism's prey preference in some cases (i.e. autotomized individuals take smaller prey and prey that is easier to handle), but it is unclear if this change has any effect on community dynamics. For example, does having predators that have lost their autotomizable limb alter prey-capture rates, and thus community-wide dynamics?

IX. CONCLUSIONS

(1) There are multiple independent origins of autotomy, as well as secondary losses, throughout Animalia. Two main hypotheses have been put forward to explain the origins of sacrificing a limb to escape predation, the intermediate-step hypothesis and the fast-latency hypothesis.

(2) Autotomizable appendages are often elaborate. Examples of autotomizable limb elaboration include bright colouration, elongation, and post-autotomy limb movement. Such elaboration has likely been selected for and/or maintained to increase the efficacy or efficiency of autotomy.

(3) There are multiple benefits associated with autotomy, including: escaping predation, escaping non-predatory entrapment, reducing the cost of injury, and increasing reproductive success. Costs of autotomy also vary among organisms. Given this variation, we modified the economic theory of escape to generate the economic theory of autotomy, which makes predictions about when an individual should autotomize.

(4) The loss of an autotomizable appendage can have a diversity of consequences on population and community dynamics. Organisms missing their autotomizable appendage generally have decreased foraging ability, are less successful at winning intraspecific fights, and are more risk averse in their habitat choice.

(5) Future research on autotomy should focus on understanding how the autotomy phenotype evolves, demonstrating the species-specific benefits and costs associated with autotomy, discerning the ecological relevance of those costs and benefits (e.g. the proportion of autotomy events used to escape predation *versus* another benefit), and quantifying the effects of appendage loss (*via* autotomy) on population and community dynamics.

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XII. SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.
Appendix S1. Stochastic character simulations reveal that autotomy and autotomizable limb elaborations have evolved multiple times throughout Animalia.

Fig. S1. Visual representation of a single stochastic character simulation for the ability to autotomize.

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