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REVIEW

To cut a long tail short: a review of lizard caudal autotomy studies carried out over the last 20 years

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Abstract

Caudal autotomy, the ability to shed the tail, is common in lizards as a response to attempted predation. Since Arnold's substantial review of caudal autotomy as a defence in reptiles 20 years ago, our understanding of the costs associated with tail loss has increased dramatically. In this paper, we review the incidence of caudal autotomy among lizards (Reptilia Sauria) with particular reference to questions posed by Arnold. We examine tail break frequencies and factors that determine occurrence of autotomy in natural populations (including anatomical mechanisms, predation efficiency and intensity, microhabitat preference, sex and ontogenetic differences, as well as intraspecific aggression). We also summarize the costs associated with tail loss in terms of survivorship and reproduction, focusing on potential mechanisms that influence fitness (i.e. locomotion costs, behavioural responses and metabolic costs). Finally, we examine the factors that may influence the facility with which autotomy takes place, including regeneration rate, body form and adaptive behaviour. Taking Arnold's example, we conclude with proposals for future research.

Introduction

Autotomy refers to the 'voluntary' shedding of a body part, a limb or an appendage, (1) usually as an anti-predator behaviour, that (2) occurs along a 'breakage plane' and (3) is controlled (i.e. the animal moves away from the trapped appendage, the loss is under some form of central neural or hormonal control or the body part is detached quickly). Caudal autotomy, or the ability to shed the tail in response to predation attack, occurs in a number of reptile taxa including tuataras, *Sphenodon* spp. (Arnold, 1984; Hoare *et al.*, 2006) and certain snakes (e.g. Cooper Jr & Alfieri, 1993; Fitch, 2003*b*; Bowen, 2004). By far the most common and best-studied examples of tail autotomy, however, are among the lizards (Suborder Sauria), where caudal autotomy is a major predator escape tactic in species within 13 of the ~20 lizard families (Downes & Shine, 2001). Caudal autotomy is an effective form of defence against predators in lizards (Arnold, 1988), significantly increasing survival of a predatory encounter (Congdon, Vitt & King, 1974; Daniels, 1985*a*; Daniels, Flaherty & Simbotwe, 1986). Loss of the tail allows the lizard to break away from a predator that has seized it by the tail, while the tail may also act as a distraction through spontaneous writhing or wriggling movements, engaging the predator's attention while the lizard escapes (Edmunds, 1974; Arnold, 1988; Pafilis, Valakos & Foufopoulos, 2005). Furthermore, some lizard species writhe or curl their tails in the presence of a predator (Mori, 1990; Vitt & Zani, 1997; Cooper Jr, 1998, 2001; Downes & Bauwens, 2002) or have brightly coloured tails, which they 'flaunt' to direct predator attacks towards the tail (Cooper Jr & Vitt, 1985; Vitt & Cooper Jr, 1986; Fitch, 2003*b*). Presumably to recoup or gain energy, some lizards (and other reptiles) may even eat their own (or another individuals') autotomized tails (Neill, 1946; Clark, 1971; Matuschka & Bannert, 1987; Gillingham, Carmichael & Miller, 1995), which in the case of *Gallotia galloti* (Lacertidae) also ensures reinfection with the parasite *Sarcocystis gallotieae*, which preferentially forms sarcocysts in tail muscle (Matuschka & Bannert, 1987).

In his comprehensive reviews of 1984 and 1988, Arnold suggested a range of costs of caudal autotomy in lizards; however, at the time these were conjectured, there was very little empirical evidence available. In particular, Arnold recognized that further research was needed to answer some key questions: studies of predation efficiency and intensity, and interpretation of tail break frequencies in natural populations, how autotomy affects individual survivorship (we will also discuss reproductive fitness), examination of costs to locomotion across taxa, the facility with which

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autotomy takes place (e.g. delicate forms vs. more robust forms) and whether individuals can alter autotomy thresholds to adapt to current circumstances. Furthermore, at the time, few studies had quantified metabolic costs of tail loss and regrowth or behavioural responses to this significant event. Subsequent to Arnold's reviews, there has been a significant amount of data collected on the topic, with numerous authors identifying and quantifying the relative costs and benefits of autotomy across lizard taxa. Herein, we synthesize data collected over the last 20 years and examine the hypothesis that despite a similar overall body plan, lizards show markedly different costs of caudal autotomy.

Tail break frequencies and factors that determine occurrence of autotomy in natural populations

Mechanisms of caudal autotomy

Arnold suggested that a greater understanding of tail break frequency in natural populations may be informative as to the costs and benefits of this process. A discussion of tail break frequencies first requires a brief discussion of the mechanisms of lizard caudal autotomy (which is described in detail elsewhere; see Etheridge, 1967; Bellairs & Bryant, 1985; Russell & Bauer, 1992). Autotomy takes place at pre-formed areas of weakness and in lizards there are two main autotomy patterns. The first is intravertebral autotomy, where transverse fracture planes (mirroring the myoseptum that separates adjacent segments of tail musculature) cross each vertebra of the central portion of the tail. The *m. caudifemoralis longus*, which is responsible for hind limb retraction, attaches to the basal part of the tail (the post-sacral or 'pygal' section) and consequently this tail section is non-autotomizing (Russell & Bauer, 1992). In fast-moving lizards (particularly those that engage in bipedal running), this muscle is large and originates from a long section of the tail; slower lizards have a smaller muscle that is attached to fewer post-sacral vertebrae (Russell & Bauer, 1992). The vertebrae in the distal tip of the tail may also lack intravertebral autotomy planes (Bellairs & Bryant, 1985). Autotomy takes place one to three vertebrae anterior to where the tail is grasped (Arnold, 1984) and therefore the animal loses the minimum amount of tail. When these lizards regenerate their lost tails, the replacement tail may or may not have a changed external morphology; internally, however, the regenerated tail has, instead of vertebrae, calcified cartilaginous tubes that lack intravertebral autotomy fracture planes (Arnold, 1984, 1988; Bellairs & Bryant, 1985) and, therefore, subsequent autotomies must take place more proximally. This mechanism has been demonstrated in a study of four populations of *Niveoscincus metallicus* (Scincidae), where the population with the highest incidence of tail breaks also demonstrated the most proximal tail breaks (Chapple & Swain, 2004*b*).

The second pattern of tail loss is via breaks between vertebrae (intervertebral autotomy): these species do not show any obvious caudal modifications relative to non-autotomizing species (Arnold, 1984). Data suggest that intravertebral autotomy is the ancestral condition (Price, 1940; Evans, 1981), and the loss of caudal autotomy has taken place in more derived forms (Arnold, 1984). Intervertebral autotomy therefore appears to be a re-evolution of caudal autotomy (Arnold, 1984).

Autotomy appears to be absent in a number of taxa, for example in some Scincidae, Corytophanidae, Iguanidae, some Phrynosomatidae, some Polychrotidae, some Tropiduridae, Crotaphytidae, Hoplocercidae, Chamaeleonidae, Xenosauridae and in the Superfamily Platynota (Varanidae, Lanthanotidae and Helodermatidae) (Fig. 1, Arnold, 1984). In addition to phylogenetic and adaptive constraints upon autotomy incidence, these observations may reflect selective pressures upon taxa that have 'actively functional' tails (*sensu* Vitt, Congdon & Dickson, 1977) where the tail is used for locomotion (e.g. is prehensile or with attachments used for climbing, or offering momentum during running or swimming) (Russell & Bauer, 1992; Zani, 1996; Russell, Bergmann & Barbadillo, 2001). Arnold (1984) cautioned that in addition to a balance of costs and benefits, the incidence of autotomy, particularly the loss of this ability, may also be subject to historical factors that may be more important than the present ones.

In contrast to invertebrates, where there is significant convergent evolution in the expression of autotomy (mechanisms and autotomizable body parts varying between taxa, Fleming, Muller & Bateman, 2007), in lizards, marked divergence in the expression of autotomy is evident. Among taxa that *do* engage in autotomy, there is a wide range of frequency of occurrence (Fig. 1), from 3% ($n = 60$) of *Callisaurus draconoides* (Phrynosomatidae) (Bulova, 1994) to 82% ($n = 216$) of *Mabuya frenata* (Scincidae) (Van Sluys, Vrcibradic & Rocha, 2002) demonstrating tail breaks or regeneration. Therefore, apart from the mechanism of autotomy, a number of other factors must influence the frequency of tail breaks in natural populations. We discuss some of the hypotheses that have been raised by Arnold and subsequent researchers to explain the range of incidence in autotomy evident for natural populations.

Predation efficiency and intensity

The first (and arguably the most important) criterion that may influence the incidence of autotomy is the degree of exposure to putative predators. An important caveat in terms of exploring predation pressure from incidence of tail loss, however, is how these data are interpreted. Greater incidence of tail loss may reflect:

(1) simply greater susceptibility to predation attack;

(2) greater inefficiency of certain predators over others, which is particularly relevant when comparing sites that may therefore have different predators present (Medel *et al.*, 1988; Chapple & Swain, 2004*b*; Cooper Jr, Pérez-Mellado & Vitt, 2004); or

(3) greater efficiency of escape through autotomy for one group over another, especially if the method of predator attack differs between these groups. For example different antipredator responses have been recorded for different sexes (Cooper Jr, 2003), age groups or body sizes (Daniels *et al.*, 1986), or even groups with different predation history (Cooper Jr, 2007) (see 'Antipredator behaviour').

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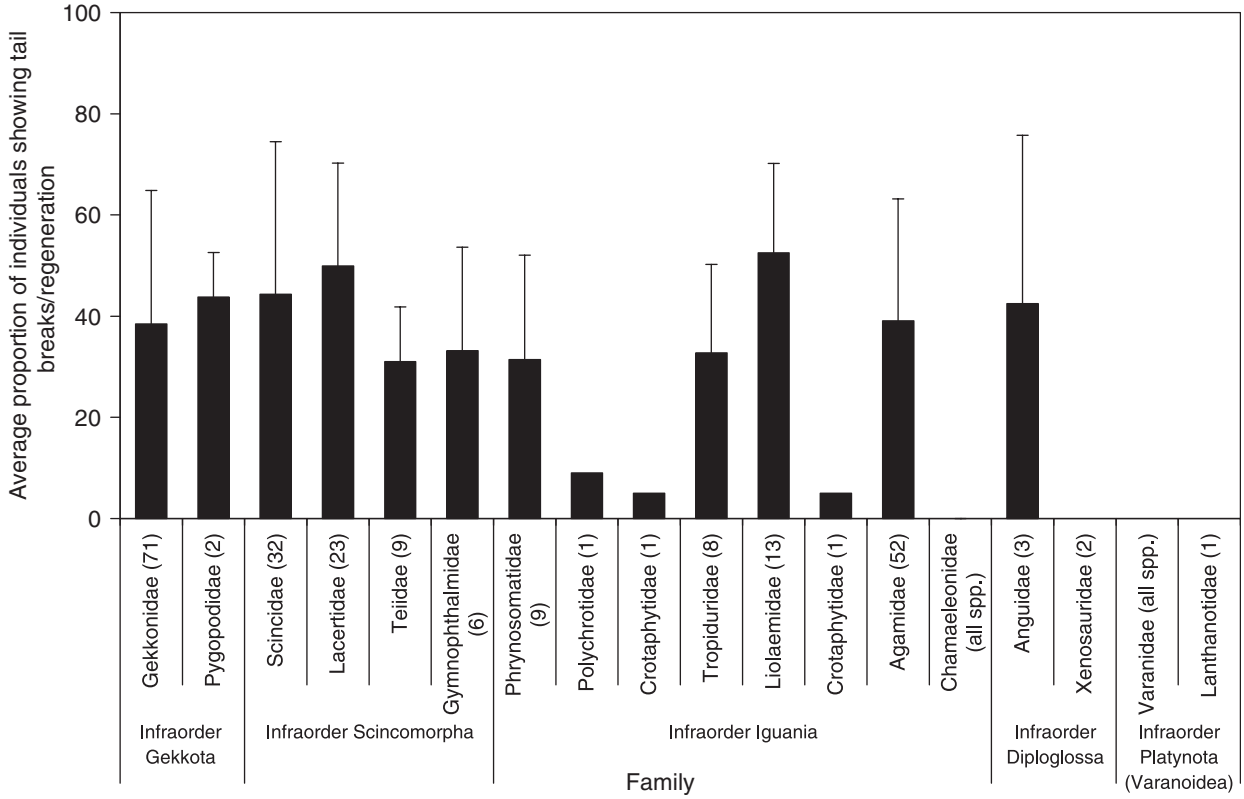

Figure 1 The incidence of tail loss in species (numbers in brackets) of 18 lizard families.

Patterns of predation efficiency and intensity have been examined in some detail for invertebrates, where differences in body size, presence of alternative defence mechanisms, type of predator and method of attack (e.g. which body part is grabbed) may all influence the efficacy of autotomy and therefore the interpretation of autotomy frequency (reviewed by Fleming *et al*., 2007). Care therefore also needs to be exercised in the interpretation of predator intensity effects on the incidence of caudal autotomy in lizards and without additional data on predator tactics or attempts, or else responses by the lizards, such data may be of little use.

For example, Diego-Rasilla (2003) report that two populations of *Podarcis muralis* (Lacertidae) in 'low' and 'high' predation sites demonstrate significant differences in autotomy frequencies (33%, $n = 21$ vs. 88%, $n = 66$, respectively), and plasticine models of lizards put out in these sites also showed (through teeth, claw and beak marks) a significantly higher incidence of attacks at the 'high' predation site. Cooper Jr *et al*. (2004) carried out a similar comparative study on another lacertid *Podarcis lilfordi* found on two Mediterranean islets with differing predation pressure. For the 'low' predation site, significantly fewer individuals show evidence of regenerated tails (50%, $n = 577$ compared with 83%, $n = 64$), autotomy was qualitatively more difficult to induce (requiring greater pressure from callipers used to hold the tail) and the autotomized tails demonstrated reduced post-autotomy movement (caused by muscle contraction). Generally, this supports the idea that populations with low predation pressure soon may lose the ability to autotomize with ease, reflecting the shift in the costs and benefits of autotomy. Additionally, fewer *P. lilfordi* voluntarily autotomized their tails and took longer to do so compared with individuals of the congener *Podarcis hispanica* found on the adjacent Iberian mainland, exposed to high predation pressure. However, despite similar body mass, *P. lilfordi* sometimes attempted to escape restraint without autotomy by rolling their bodies and biting, a behaviour not shown by *P. hispanica*, possibly reflecting a difference unrelated to predation pressure *per se*, but either type of predation, other selective pressures (such as different microhabitats available at the different sites) or historical phylogenetic differences. These studies demonstrate that studying predators as well as the responses of lizards to such predation pressure together may be helpful in determining patterns of autotomy frequency in natural populations.

Effect of habitat on incidence of autotomy

Before Arnold's reviews of 1984 and 1988, there had been several studies examining the influence of habitat and microhabitat on autotomy frequency. For example, Jaksić & Fuentes (1980), Pianka & Pianka (1976) and Pianka & Huey (1978) recorded higher autotomy frequencies among species assemblages for those species that used more exposed or higher (e.g. trees or rocks) microhabitats. Since then, Tanner & Perry (2007) found that Galápagos lava

lizards *Microlophus albemarlensis* (Tropiduridae) living near roads show a high autotomy frequency (29%, $n = 31$), while those further from the road (despite an increase in population density) show a low autotomy frequency (<1%, $n = 272$). Animals occupying territories near the road use the road for thermoregulation and are therefore more exposed to predators, feral animals, bicycles, human foot and vehicle traffic. By contrast, Smith (1996) has reported no effect of habitat (woods vs. rock and gravel slopes) on the total autotomy frequency of *Sceloporus virgatus*, but did find that juveniles had lower autotomy frequencies than adults in the woods and a higher frequency on the slopes, suggesting different predation or use of cover at these sites. Furthermore, Van Sluys *et al*. (2002) were surprised to find that an active (albeit secretive) forager (*M. frenata*, Scincidae) had a higher autotomy frequency than did a syntopic ambush forager that uses exposed perches (*Tropidurus itambere*, Tropiduridae), and explained the difference as being due to phylogenetic differences in autotomy ability.

Clearly, therefore, results of microhabitat studies can be contradictory and an important consideration is how the behaviour of individuals changes as a *consequence* of tail autotomy (Martín & Salvador, 1992, Martín & Salvador, 1993*a*) (see 'Do tailless lizards change their behavioural responses?'). Tailless individuals may become more cryptic, utilize different substrates and, within reason, move to different environments. Microhabitat selection and behaviour are therefore important considerations in interpreting these data.

Sex differences and intraspecific aggression

A few studies have indicated gender differences in terms of the incidence of tail loss. For example, in *Mabuya heathi* (Scincidae) (Vitt, 1981), males demonstrate a higher incidence of tail loss than females of the same size. However, the majority of researches to date suggest no significant sex difference in lizard tail loss frequency: for example, *Sceloporus* spp. (Phrynosomatidae) (Vinegar, 1975), *Tr. itambere* (Tropiduridae) (Van Sluys *et al*., 2002), and three skink species *M. frenata* (Van Sluys *et al*., 2002), *N. metallicus* (Chapple & Swain, 2002*a*, 2004*b*) and *Eumeces chinensis* (Lin, Qu & Ji, 2006). This lack of sex difference may be despite obvious morphological differences between the sexes. For example, Jaksić & Fuentes (1980) record that sexual dimorphism is not correlated with significant differences in tail loss for 12 *Liolaemus* species (Liolaemidae), and Fobes *et al*. (1992) found no difference in autotomy frequency between the sexes of *Anolis cybotes* (Polychrotidae), despite the males being larger and utilizing higher perch sites (see 'Effect of habitat on incidence of autotomy').

Although autotomy is mostly associated with escape from predation, it is likely that aggression from conspecifics also causes tail loss. Firstly, as there is a well-established link between size and dominance in lizards (Tokarz, 1995) and removing a tail makes a lizard appear smaller, it could be adaptive for males to attempt to remove the tails of rival males. This is an area where we have found no recent data. Indirect evidence is available for *Uta stansburiana* where a higher incidence of tail loss is evident among subordinate than dominant males (Fox, Rose & Myers, 1981). Other reasons, however (apart from intraspecific aggression), could also account for these differences. Secondly, if the tail is used as a social signal or during aggression, then individuals would be at an advantage if they could induce tail loss in a rival. Intraspecific aggression has been linked to autotomy (sometimes followed by cannibalism of shed tails) in *G. galloti* (Lacertidae) (Matuschka & Bannert, 1987), *Thecadactylus rapicauda* (Gekkonidae) (Vitt & Zani, 1997) and *Ctenotus fallens* (Scincidae) (Jennings & Thompson, 1999). Similar tail loss frequencies have been recorded for males as well as females of all three species. However, while both male and female *G. galloti* and *Ct. fallens* engage in conflict, female *Th. rupicauda* do not fight (but yet show similar tail loss frequencies as males). Few authors record where intraspecific aggression does not result in caudal autotomy (e.g. *Po. muralis* Brown, Taylor & Gist, 1995). The link between intraspecific conflict and tail autotomy is an interesting one because it suggests that a mechanism that is advantageous for escape from predation may also be used during intraspecific conflict (e.g. Jennings & Thompson, 1999). If a tail is used as a weapon, then it would be advantageous for an individual not to autotomize its tail during combat, which could result in conflicting selective pressures; we are not aware of any species that uses its tail as a weapon and yet still drops their tail as a means of predator avoidance. This is an area where future research utilizing experimental manipulation of populations of lizards could provide rewarding data.

Agama agama (Agamidae) males use their tails to whip rivals (Harris, 1964) and may induce autotomy in them. Paradoxically, loss of a tail may eventually also provide a social benefit. Male and female *A. agama* observed in Sierra Leone have different regenerated tail shapes: compared with females, more males regenerate tails that develop a 'club' on the tail rather than the more usual tapered shape. Although this may result from (unidentified) different types of injury that males and females receive, Schall *et al*. (1989) suggest that clubbed tails may have an adaptive advantage for the males. The tails are used as whips in agonistic encounters between males and a clubbed tail would be more effective in such an encounter than a tapered tail. Arnold (1984) notes that any variation in the benefits of autotomy would be just as significant as variation in costs and these findings may be excellent examples of this observation.

Ontogenetic differences

Tail autotomy may have physiological and behavioural impacts that differ according to a lizard's age and stage of development. A juvenile lizard that loses its tail not only needs to direct energy towards regeneration but also towards somatic growth; behavioural and physiological changes may therefore be more extreme for juveniles than for adults.

Although various authors have recorded differences in the frequency of tail breaks between different age groups,

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these data should be interpreted with caution. A first caveat is that, due to the loss of intravertebral autotomy planes in regenerated tails, subsequent autotomies will take place more proximally, and even if it has undergone multiple autotomy events, an animal will still appear to have a single tail break. Therefore, although autotomies will intuitively accumulate over time [older individuals are more likely to have undergone an autotomy event(s)], it may not be possible to determine age differences in susceptibility at a single point in time. Secondly, predation is likely to have different impacts upon juveniles and adults. Daniels *et al.* (1986) very clearly demonstrated that juvenile *Christinus marmoratus* are more susceptible to a small mammalian predator (74% capture rate) compared with adults (24% capture rate), and while 62% of adults used autotomy to escape from this predator, only 7% of juveniles did so. Therefore, although incidences of tail autotomy may differ between age groups (e.g. Vitt *et al.*, 1977), antipredator behaviour coupled with differences in predator technique make the observation of tail break frequency among survivors a difficult message to interpret. Behaviour and habitat preferences may therefore differ between cohorts and longitudinal studies may be fruitful in this respect. An alternative may be to compare incidences of tail breaks between similar-aged animals in different populations. For example, Brandl & Völkl (1988) report that adult *Podarcis* (= *Lacerta*) *dugesii* force juveniles into suboptimal habitats with fewer refuges, such that in high-density populations, juveniles have the highest autotomy frequencies.

The use of autotomy may vary markedly with age. For example, some lizard species show distinctive dichromatism between juveniles and adults. Generally *Eumeces* spp. (Scincidae) juveniles have bright blue tails; only a few species retain this coloration as adults and most fade to dull cryptic colours after sexual maturity (Vitt & Cooper Jr, 1986). The most common explanation for this ontogenetic change is that the bright tail acts as some form of defence for the juveniles: either the coloration increases the chance of surviving a predator attack by directing the attack at the tail, the bright tail inhibits attack from conspecific adults or the tail is an aposematic signal (Cooper Jr & Vitt, 1985). All these hypotheses have received some support (Cooper Jr & Vitt, 1985; Hawlena *et al.*, 2006); however, if all these explanations are at least partly true, why do adults not need bright tails, because they would also benefit from a predator distracting tail (Clark & Hall, 1970)? Vitt & Cooper Jr (1986) suggest that adults and juveniles may face different risks, a theory that has recently been tested in *Acanthodactylus beershebensis* (Lacertidae) (Hawlena *et al.*, 2006). The authors found that hatchlings, which flaunt their bright blue tail, forage more actively and spend more time in open microhabitats (where there is greater risk of predation) than 3-week-old juveniles that have lost the blue coloration. Another lacertid, *Mesalina guttulata*, found in the same habitat does not show an age-related dichromatism, but also shows no age-related differences in foraging behaviour (Hawlena *et al.*, 2006). By contrast with *Eumeces* species, which flaunt their tail, *Cnemidophorus sexlineatus* hatchlings also have a blue tail but do not flaunt it (Fitch, 2003*a*). This suggests that hatchlings of these species not only face different predation pressures to adults, but there may also be interspecific differences in predation pressure. Although it demonstrates a highly developed autotomy ability, *Ophisaurus attenuatus* does not show adult/offspring dichromatism, suggesting that adults and hatchlings face the same predation pressures and deal with them in the same way through crypsis (Fitch, 2003*a*).

In addition to tail loss, other antipredator behaviour also varies with ontogeny. Kelt, Nabors & Forister (2002) report that large tailless *Liolaemus nigromaculatus* are more tolerant of approach by an observer compared with intact individuals, although this pattern was not evident for small- or intermediate-sized animals. The authors suggest that these results demonstrate size-dependent differences in terms of (1) the effects of tail autotomy on mobility or energy use; (2) level of exposure to different types of predators; (3) that larger, older animals (that had undergone an autotomy event) learn to respond differently to predators.

There is evidence that the incidence of autotomy may reflect the developmental fitness of individuals. Seligmann, Beiles & Werner (2003) found that among 193 species from various lizard families (as well as the tuatara), morphologically directional asymmetries of the feet (indicating left side 'handedness') had a higher frequency of damaged tails than those with 'handedness' to the right. The authors suggest that left-handedness may be correlated with a lower level of developmental stability and therefore fitness.

Finally, some non-autotomizing taxa (e.g. iguanids, some skinks) demonstrate loss of vestigial fracture planes as they grow older (Arnold, 1984). The developmental loss of intravertebral autotomy in these groups could reflect differences in susceptibility to predation for small (young) compared with larger (old) individuals, especially for large species (see 'Predation efficiency and intensity'); a potential link with ontogenetic dietary shifts (e.g. Chapple, 2003) also warrants further investigation. In some of these species (e.g. *Tiliqua* skinks), juveniles can autotomize tails but apparently do not regenerate them (pers. obs., Arnold, 1984; Fenner, Hutchinson & Bull, 2006).

How does autotomy affect individual fitness?

Repeated loss of the caudal autotomy response across taxa implies that, along with the obvious benefits of tail autotomy, tail loss also carries significant costs, summarized in Fig. 2 (Arnold, 1988; McConnachie & Whiting, 2003). Many lizards are influenced by:

(1) the loss of their tail itself in terms of costs to locomotion, susceptibility to predation and social impacts;
(2) costs associated with regenerating the lost tissue; as well as
(3) indirect effects of tail loss on behaviour.

For many studies it is not possible to identify a single cost associated with taillessness, particularly for species where caudal autotomy significantly compromises locomotion and therefore other behaviour subsequently; generally, it should be

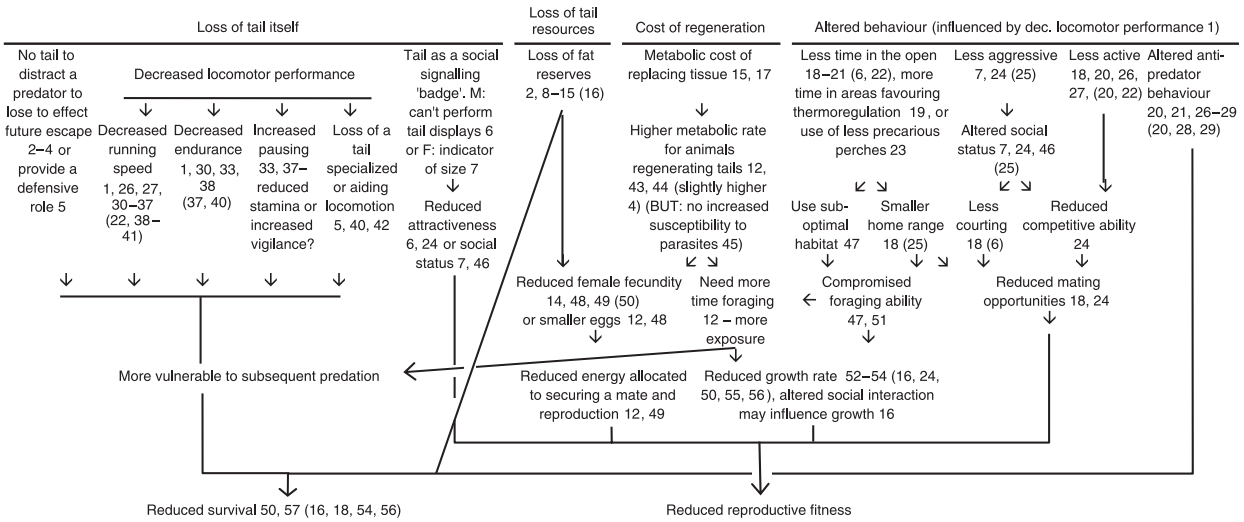

Figure 2 Summary of literature data for the costs of tail autotomy in lizards. References that have found no cost, or an exception to such cost are indicated in brackets. References are: 1, Chapple & Swain (2002*a*,*b*); 2, Daniels *et al.* (1986); 3, Daniels (1985*a*,*b*); 4, Congdon *et al.* (1974); 5, Bauer & Russell (1994); 6, Langkilde *et al.* (2005); 7, Fox *et al.* (1990); 8, Avery (1970); 9, Arnold (1988); 10, Doughty *et al.* (2003); 11, Chapple & Swain (2002*a*); 12, Dial & Fitzpatrick (1981); 13, Daniels (1984); 14, Chapple *et al.* (2002); 15, Vitt *et al.* (1977); 16, Althoff & Thompson (1994); 17, Bellairs & Bryant (1985); 18, Salvador *et al.* (1995); 19, Martín & Salvador (1992); 20, Cooper Jr (2003); 21, Cooper Jr (2007); 22, McConnachie & Whiting (2003); 23, Ballinger (1973); 24, Martín & Salvador (1993*a*,*b*); 25, Kaiser & Mushinsky (1994); 26, Formanowicz *et al.* (1990); 27, Downes & Shine (2001); 28, Capizzi *et al.* (2007); 29, Kelt *et al.* (2002); 30, P. A. Fleming *et al.* (unpubl. data); 31, Ballinger *et al.* (1979); 32, Punzo (1982); 33, Martín & Avery (1998); 34, Shine (2003); 35, Cooper Jr *et al.* (2004); 36, Pond (1978); 37, Lin & Ji (2005); 38, Daniels (1985*b*); 39, Daniels (1983); 40, Brown *et al.* (1995); 41, Huey *et al.* (1990); 42, Medger *et al.* (2008); 43, Naya *et al.* (2007); 44, Naya & Bozinovic (2006); 45, Oppliger & Clobert (1997); 46, Fox & Rostker (1982); 47, Martín & Salvador (1993*b*); 48, Smyth (1974); 49, Wilson & Booth (1998); 50, Fox & McCoy (2000); 51, Martín & Avery (1997); 52, Smith (1996); 53, Ballinger & Tinkle (1979); 54, Niewiarowski *et al.* (1997); 55, Vitt & Cooper Jr (1986); 56, Webb (2006); 57, Wilson (1992).

considered that multiple factors may influence fitness in tailless lizards. As measures of Darwinian fitness, both reduced survival and reduced reproductive output (e.g. reduced female fecundity, smaller eggs, reduced mating opportunities) have been recorded in autotomized lizards by various authors. We discuss different physiological and behavioural components that may contribute towards these findings in the following section.

Are there differences in autotomy locomotion costs across taxa?

For many lizard species, locomotor performance may be compromised by caudal autotomy. Firstly, in terms of speed, various species demonstrate a decrease in running speed (Pond, 1978; Ballinger, Nietfeldt & Krupa, 1979; Punzo, 1982; Formanowicz, Brodie & Bradley, 1990; Martín & Avery, 1998; Downes & Shine, 2001; Chapple & Swain, 2002*b*; Shine, 2003; Cooper *et al.*, 2004; Lin & Ji, 2005; P. A. Fleming *et al.*, unpubl. data). Compromised escape speed is not a universal phenomenon, however, and some animals are not slowed by tail loss (Daniels, 1983, 1985*b*; Huey *et al.*, 1990; Brown *et al.*, 1995; McConnachie & Whiting, 2003; Chapple, McCoull & Swain, 2004; Lin & Ji, 2005). In fact, *Ch. marmoratus* geckos (Daniels, 1983) and *Po. muralis* lacertids (Brown *et al.*, 1995) actually become faster in escape over horizontal surfaces after loss of their tail. For the geckos, it is suggested that because they store fat in their tails, they are lighter and experience reduced friction with the substrate after tail loss (Daniels, 1983). Brown *et al.* (1995) interpret the lizards' faster responses as reflecting differences in antipredator strategies.

A second aspect of locomotory performance is decreased endurance after tail autotomy (Daniels, 1985*b*; Martín & Avery, 1998; Chapple & Swain, 2002*b*; P. A. Fleming *et al.*, unpubl. data, but see Brown *et al.*, 1995; Lin & Ji, 2005). Tailless lizards may increase the amount of times that they pause during exercise, which may reflect reduced stamina or increased vigilance (Martín & Avery, 1998; Lin & Ji, 2005). Although it is probably not possible to identify a single cause of reduced stamina, it may reflect increased effort required to run without a tail, loss of energy substrate due to tail loss or else compromised physical state (e.g. a link has been demonstrated for tick infestations and running stamina: Main & Bull, 2000). Gravidity may result in females being slower and having less stamina (Shine, 1980; Cooper Jr *et al.*, 1990; Olsson, Shine & Bak-Olsson, 2000; Wapstra & O'Reilly, 2001). Although it seems intuitive that females, especially gravid ones, will incur a greater locomotory impact from autotomy, this effect needs to be placed in the context of other factors affecting these animals. For example, Shine (2003) has demonstrated that pregnancy

significantly impairs locomotion in *Lampropholis guichenoti* (Scincidae); however, a large meal, a temperature decrease of about 5 °C or autotomy of part of the tail would produce a similar decrease in running speed. In fact, tail loss substantially reduced speeds (31%) of non-gravid females, but not for gravid females. In *N. metallicus* (Scincidae), the locomotory costs of autotomy are limited, the most important effects being a reduction in endurance in females and in sprint speed in males (Chapple & Swain, 2002*b*). The females rapidly regain their endurance capacity; males, however, did not recover their sprinting ability over the course of the experimental period (12 weeks), despite regenerating 45–50% of their original tail length (Chapple & Swain, 2002*b*).

Thirdly, many lizards use their tail during locomotion. As a base for muscle attachment (see 'Mechanisms of caudal autotomy'), the tail may therefore provide momentum and balance. Individuals must therefore correct for the disequilibrium caused by tail loss at each step; for example, loss of stride length (Martín & Avery, 1998), stability (Ballinger, 1973; Daniels, 1985*b*; Brown *et al*., 1995), thrust or momentum (Daniels, 1985*b*) may all be consequences of caudal autotomy. The water skink *Eulamprus quoyii*, for example, uses its tail in order to swim and swimming speed almost halves in tailless individuals (Daniels, 1985*b*). Other lizards have a tail that performs some other vital role such as being prehensile or having an adhesive pad(s) (Bauer & Russell, 1994). *Anolis carolinensis* (Polychrotidae) uses its tail to stabilize it when escape jumping; autotomized individuals show high variation in their body angle and reduced jump distances (Bonvini, 2007). The Cape dwarf gecko *Lygodactylus capensis* (Gekkonidae) uses its tail normally as a prop, stabilizing the hind part of the body and maintaining contact with the substrate; tail loss therefore significantly reduces the ability of these animals to climb vertically (Medger, Verburgt & Bateman, 2008). Notably, however, even without specialization, a tail can assist in balance. For example, Brown *et al*. (1995) tested the ability of *Po. muralis* to traverse a 'tight rope' and found that tailless individuals were significantly compromised in terms of both speed and distance travelled over this obstacle.

Finally, an element of the perception of danger should be taken into account in terms of understanding locomotion responses by lizards post-autotomy. Brown *et al*. (1995) recorded that *Po. muralis* individuals that have lost their tail a second time are faster than lizards that have autotomized for the first time. One explanation is that the regenerated tail is in some way different from the original, and the animal may therefore physically adapt to having a more cumbersome appendage. However, the authors interpreted this finding as a form of learning response, a finding that warrants further investigation in other species.

Do tailless lizards change their behavioural responses?

Lizards will often significantly alter their behaviour in response to tail autotomy. Many of these changes are an indirect result of decreased locomotor performance due to tail autotomy (Chapple & Swain, 2002*b*); however, altered behaviour has also been recorded without a concomitant measurement of reduced locomotory ability. Although Arnold (1988) was aware of the compromised situation for tailless lizards in terms of no longer having a tail to lose or for predator distraction, few behavioural changes in response to caudal autotomy had been measured at that stage.

Antipredator behaviour

In addition to altered habitat use (see 'Habitat selection and foraging'), more specific antipredator responses are altered in tailless lizards. There are differences in how close they will allow a putative predator (i.e. the researcher) to approach before responding or how far they will run after they have been startled. Flight initiation distance (i.e. the linear distance between the approaching predator and the lizard at the time of the lizard's first movement in response to the predatory attack) has been examined for a number of species. For some, shorter flight initiation distance for tailless lizards has been recorded compared with intact individuals (i.e. tailless individuals allow a putative predator to approach much closer before they try to escape – presumably, they are relying on crypsis until it is clear that the predator has definitely observed them). For example: *Zootoca vivipara* (Lacertidae) (Capizzi, Luiselli & Vignoli, 2007), *Scincella lateralis* (Scincidae) (Formanowicz *et al*., 1990) and large male *Li. nigromaculatus* (Liolaemidae) (Kelt *et al*., 2002). By contrast, no difference in flight initiation distance has been recorded for *Iberolacerta horvathi* (Lacertidae) (Capizzi *et al*., 2007), *Holbrookia propinqua* (Phrynosomatidae) (Cooper Jr, 2003) or small- or medium-sized male *Li. nigromaculatus* (Kelt *et al*., 2002). Finally, for a few species, tailless individuals actually have longer flight initiation distances. Tailless *La. guichenoti* (Scincidae) are more susceptible to a diurnal snake (*Demansia psammophis*, Elapidae) than are intact conspecifics, due to compromised locomotor performance and their tendency to flee sooner from an approaching predator, thus eliciting attack by the visually hunting snake (this different behaviour did not make them more susceptible to a nocturnal elapid, *Rhinoplocephalus nigrescens*, which forages more on chemoreception, Downes & Shine, 2001). Longer flight initiation distances have also been recorded for *S. virgatus* the day following autotomy (Cooper Jr, 2007). However, Cooper Jr (2007) notes that captured but non-autotomized lizards also demonstrated longer flight initiation distances, suggesting that the lizards perceive an increased risk of predation, regardless of whether they had lost their tail in the encounter. Had the effects of capture not been assessed, increased distance fled might erroneously have been considered due to the effects of autotomy alone (Cooper Jr, 2007), which is a very important consideration for future studies of antipredator responses in lizards post-autotomy. An analogous situation has been recorded for limb autotomy in the cricket *Gryllus bimaculatus* (Gryllidae), where singing males faced

three different levels of disturbance (disturbance, disturbance involving handling the insect and disturbance culminating in autotomy of a hind leg) (Bateman & Fleming, 2006). Latency to sing after disturbance the following day was not different for the animals that were simply disturbed, but was higher for the two levels where animals were handled the day before; this high latency was maintained for a third day only in the autotomized males, suggesting perception of higher predation and lowered locomotory ability (Bateman & Fleming, 2006).

As a second measure of antipredator response, tailless animals may also flee a different distance compared with intact animals. Tailless *H. propinqua* (Phrynosomatidae) stay closer to cover, and tailless males (but not females) flee further when approached by an investigator stimulating a predator (Cooper Jr, 2003). Tailless *S. virgatus* also flee further upon disturbance, and are also more likely to enter refuge (Cooper Jr, 2007).

Habitat selection and foraging

Lizards can change their habitat selection post-autotomy. For example, due to compromised mobility and balance, tailless lizards may utilize sites that are less precarious (Ballinger, 1973), select areas favourable for thermoregulation (Martín & Salvador, 1992), presumably to speed up regeneration and recovery processes, or use sub-optimal habitat (Martín & Salvador, 1993*a*) in particular areas with greater cover availability as a measure to avoid potential conflict or reduce exposure and therefore predation risk (Martín & Salvador, 1992; Salvador, Martín & López, 1995; Cooper Jr, 2003, 2007; Langkilde, Alford & Schwarzkopf, 2005, but see: McConnachie & Whiting, 2003). Lizards may also become less active as a result of tail loss (Formanowicz *et al*., 1990; Salvador *et al*., 1995; Downes & Shine, 2001; Cooper Jr, 2007, but see: Cooper Jr, 2003; McConnachie & Whiting, 2003).

Altered behaviour may serve to improve their chances of survival, but can also incur costs. For example, the loss of locomotor ability could reduce an animal's foraging and prey capture abilities (Martín & Salvador, 1993*a*; Martín & Avery, 1997). Compromised foraging ability (Martín & Salvador, 1993*a*), leading to greater time needed for foraging (Dial & Fitzpatrick, 1981), could lead to increased exposure to predators, thereby reducing survival. Reduced feeding rate and thereby reduced growth rate (Ballinger & Tinkle, 1979; Smith, 1996; Niewiarowski *et al*., 1997) but see: (Vitt & Cooper Jr, 1986; Martín & Salvador, 1993*b*; Althoff & Thompson, 1994; Fox & McCoy, 2000; Webb, 2006) may have an impact upon reproductive fitness (e.g. less energy available for reproduction) or survival (less fat reserves).

Social behaviour and reproduction

There are also social costs to losing tails (which can differ between the sexes). For example, tail loss can result directly in reduced attractiveness: upon loss of their tails, male *Carlia jarnoldae* (Scincidae) can no longer perform tail displays (Langkilde *et al*., 2005), while female *U. stansburiana* (Phrynosomatidae) use males' tails as an indicator of their size and therefore fitness (Fox, Heger & Delay, 1990). Animals that become less active may consequently become less aggressive and therefore less competitive (Fox *et al*., 1990; Martín & Salvador, 1993*b*, but see: Kaiser & Mushinsky, 1994). Male *Lacerta monticola* (Lacertidae) experience reduced social status after autotomy (intact males dominate tailless males in agonistic encounters), and they also secure fewer courtships and copulations (Martín & Salvador, 1993*b*). By contrast, tailless females are courted by the same number of males as intact females, but mate less; this may be due either to males interpreting a tailless female as having fewer resources to invest in clutches, or that the females choose not to mate when tailless as they are directing resources towards tail regeneration (Martín & Salvador, 1993*b*). In *Psammodromus algirus* (Lacertidae), tail autotomy in large dominant males results in a reduction in their home range, a reduction in the number of females within the home range and therefore a reduction in mating opportunities (Salvador *et al*., 1995). As a corollary of this, however, smaller, subordinate intact neighbouring males may gain an increase in mating opportunities (Salvador *et al*., 1995). Furthermore, Kaiser & Mushinsky (1994) report that tail loss may be of minor consequence to *Anolis sagrei* (Polychrotidae) males if they have already established a territory, suggesting that the impacts of tail autotomy will vary depending on established social hierarchies. Finally, altered social interaction may influence growth and therefore potentially survivorship or reproductive output (e.g. *U. stansburiana* Phrynosomatidae: Althoff & Thompson, 1994).

Are there metabolic costs of tail loss and regrowth?

When a lizard autotomizes its tail, all resources (i.e. fat reserves) stored in the tail are also lost (Avery, 1970; Vitt *et al*., 1977; Dial & Fitzpatrick, 1981; Daniels, 1984; Daniels *et al*., 1986; Arnold, 1988; Chapple, McCoull & Swain, 2002; Chapple & Swain, 2002*a*; Doughty, Shine & Lee, 2003, but see: Althoff & Thompson, 1994, reviewed by Bernardo & Agosta, 2005). In the short term, lizards may therefore have to change energy substrate use. Further to lost resources, the long-term metabolic cost of regenerating the tail imparts an additional energetic burden upon the animal (McConnachie & Whiting, 2003). A study of four populations of *N. metallicus* demonstrated that the population with the greatest number of tail breaks (and more proximal tail breaks) was also smaller, which could be an indirect reflection of the energetic burden of repeated caudal autotomy and tail regeneration in this population (Chapple & Swain, 2004*b*).

To date, few studies have addressed the metabolic costs of caudal autotomy in lizards. It may be difficult to distinguish between the costs associated with loss of resources in the tail and the cost of replacing the tissue due to the immediate inception of tail regeneration; however, any increased

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energetic burden is likely to contribute towards long-term costs of caudal autotomy. In terms of resting metabolic rate, higher values have been recorded for three lizard species during tail regeneration (*Coleonyx brevis* Gekkonidae, Dial & Fitzpatrick, 1981, *Liolaemus nitidus* Liolaemidae, Naya & Bozinovic, 2006, *Liolaemus belli*, Naya *et al*., 2007), but no differences for two other gecko species (*Coleonyx variegatus* Gekkonidae, Congdon *et al*., 1974, *Ly. capensis* Gekkonidae, P. A. Fleming *et al*., unpubl. data). Only one study has examined the interaction of tail loss with costs of locomotion to date: immediately (2 days) post-autotomy, *Ly. capensis* demonstrate reduced metabolic expenditure (measured as CO_2 production) during locomotion (independent and additive to reduced speed and distance covered), which may reflect loss of energy substrate along with tail loss or the removal of metabolically active tail tissue (P. A. Fleming *et al*., unpubl. data).

Although metabolic rate (and therefore ability to speed up tail regeneration) is closely linked to body temperature in poikilotherms, no change in thermoregulation patterns has been recorded for *Z. vivipara* (Lacertidae) (Herczeg *et al*., 2004), *N. metallicus* (Scincidae) (Chapple & Swain, 2004*a*) and *E. quoii* (Scincidae) (Wilson, 1994) at various stages of regenerating tails. By contrast, *La. monticola* (Lacertidae) increase their basking event duration, and alter basking sites after tail loss (Martín & Salvador, 1993*c*). Similarly, after autotomy, female *H. propinqua* (Phrynosomatidae) are more likely to be seen than males, which may reflect that while tailless individuals of both sexes need to obtain energy for tail regeneration, females need additional energy to invest in their developing clutches and are required to both forage and bask to aid embryonic development (Cooper Jr, 2003). Finally, while it might be expected that autotomized animals may have compromised health, in fact there is no increased susceptibility to parasites in tailless *Z. vivipara* (Lacertidae), although tail regeneration is compromised by parasitism (Oppliger & Clobert, 1997).

Energetic costs and reproduction

The reduction in energy stores due to tail loss or regeneration can have a significant effect on energy able to be allocated to various activities, including securing a mate and reproduction (reviewed by Bernardo & Agosta, 2005). Reduced female fecundity has been recorded in various species (Smyth, 1974; Wilson & Booth, 1998; Chapple, McCoull & Swain, 2002, but see: Fox & McCoy, 2000) and females may produce smaller eggs as a consequence of tail loss (Smyth, 1974; Dial & Fitzpatrick, 1981).

Storing fat deposits in the tail, where they may be readily lost through caudal autotomy, seems paradoxical, and tail loss may have a severe impact on species with minimal abdominal fat deposits. The relationship between female reproductive effort and caudal autotomy has been examined by a number of authors, and the location of fat stores has been raised as an important consideration in these studies (reviewed by Bernardo & Agosta, 2005). For example, four species of skink demonstrate significant decreases (42–75%) in clutch size as a result of tail loss (*Eulamprus tympanum* Doughty & Shine, 1997, 1998, *Hemiergis peronii* Smyth, 1974, *Ctenotus taeniolatus* Taylor, 1986, *E. quoyii*, Wilson & Booth, 1998), and females may also skip reproduction entirely (Bernardo & Agosta, 2005). Smaller litters are probably due to the redirection of energetic resources into tail regeneration. Much smaller reductions in clutch size are evident for two other skinks (17.5%: *N. metallicus* Chapple *et al*., 2002, 14%: *Morethia boulengeri* Smyth, 1974) or *Co. brevis* geckos (Dial & Fitzpatrick, 1981) which have abdominal fat stores in addition to tail storage, while no measurable effect is recorded for *La. guichenoti* (Taylor, 1984) or *U. stansburiana* (Fox & McCoy, 2000), which similarly have multiple sites for fat storage. In *U. stansburiana,* there was also no difference for males in terms of testes mass (Fox & McCoy, 2000). However, even species with substantial caudal fat deposits may still reduce autotomy impacts due to the location of these reserves in the proximal portion of the tail, which will not be autotomized (Chapple & Swain, 2002*a*; Lin & Ji, 2005).

Survival

Tail autotomy may directly reduce survival: animals may be more susceptible to future predation attacks because they no longer have a tail to either distract a predator or lose in order to effect escape (Congdon *et al*., 1974; Daniels, 1985*a*; Daniels *et al*., 1986) or have altered antipredator responses (see 'Antipredator behaviour'). Furthermore, reduced fat storage coupled with the necessity of regrowing a new tail could impair an individual's survival if exposed to physiologically stressful conditions. However, contradictory data exist in this regard. For example, the survival rate of *U. stansburiana* with varying levels of tail completeness (Wilson, 1992) or else those that had been induced to autotomize their tail the previous autumn (Fox & McCoy, 2000) is significantly reduced compared with that of intact animals. However, other authors record no effect of caudal autotomy upon survival of hatchlings of this species (Niewiarowski *et al*., 1997) or equally low survivorship of adults (Althoff & Thompson, 1994). Differences between such studies (the second and third study were even carried out at the same location) are enlightening, because they suggest ontogenetic and temporal differences in the effect of caudal autotomy upon survivorship.

As for the finding for hatchling *U. stansburiana* (Niewiarowski *et al*., 1997), no significant effect of autotomy of survivorship has been found for hatchling (Civantos, Salvador & Veiga, 1999) or adult (Salvador *et al*., 1995) *Ps. algirus* (Lacertidae). Similarly, no significant differences were recorded for *Oedura lesueurii* (Gekkonidae) juveniles that autotomized their tails during capture compared with those that did not (Webb, 2006).

Does the facility with which autotomy takes place vary?

Regeneration rate

It might be expected that ease of autotomy or readiness to autotomize would vary in response to the speed of tail regeneration, because rapid replacement of the tail would mitigate potentially negative impacts of the loss. However, very few authors have examined this potential relationship. Arnold (1984) discussed the considerable differences in regeneration rate. He recorded that low regeneration rates appear to be most frequent in elongate (usually legless) lizards that are fossorial, live close to the earth–vegetation interface or under objects. Legless (or reduced leg) lizards (i.e. some Anguidae, some Scincidae, Pygopodidae and Anniellidae) use their whole bodies for serpentine movement or burrowing and may therefore pay little locomotory cost from tail loss (Arnold, 1984). If these animals do not undergo markedly reduced short-term fitness (i.e. survivorship) from autotomy, then rapid regeneration may be less important than body growth or other fitness factors (Arnold, 1984). However, many taxa with completely different body forms also show little or nil regeneration of damaged tails (see 'Mechanisms of caudal autotomy'); a different explanation is therefore warranted for these taxa. For example, Bernardo & Agosta (2005) suggest that regeneration rate could be related to lifespan. Over the last 20 years, researchers have investigated the physiology of regeneration (e.g. Ndukuba & Ramachandran, 1989; Oppliger & Clobert, 1997; Clause & Capaldi, 2006; Naya & Bozinovic, 2006, Naya *et al*., 2007), but we have been unsuccessful in finding studies that have examined ecological or adaptive explanations of differences in tail regeneration rates between different lizard taxa. Investigation of the factors influencing relative rates of regeneration in other lizard taxa would be worthy of further study.

Delicate versus more robust species

When discussing the range of costs of autotomy, Arnold (1988) suggested that more empirical investigation into the facility with which autotomy takes place between different lizard body types should be carried out. He predicted that, because delicately constructed lizards have a limited ability to fight back, 'use of the tail to divert attack from the head and body will be more important' by comparison with more robust species that have teeth and claws to fight off a predator. Although Dial (1978) found that of two sympatric geckos, the larger, more aggressive species (*Coleonyx reticulatus*) had a lower frequency of tail breaks than did the smaller one (*Co. brevis*) (supporting Arnold's suggestion), this hypothesis still requires further investigation. Few data have been gathered over the last 20 years that address this question; partially, this may reflect the difficulty in designating what is 'robust' and what is 'delicate' or 'gracile' among lizards.

Can individuals alter autotomy thresholds to adapt to current circumstances?

Of all the questions raised by Arnold (1988), this may be the most difficult to answer, and yet is arguably the most interesting. It is difficult to see how ontogenetic differences in willingness to lose a tail can be interpreted: because adults are so much larger than juveniles it would naturally be expected that greater force is required to autotomize adults' tails. Comparison of similar life stages seems more appropriate, and latency time to voluntary autotomy (e.g. Cooper Jr *et al*., 2004) seems an appropriate measure.

Arnold (1984) observed that autotomy is harder to induce in anaesthetized than conscious animals, and that captive 'tame' lizards will tolerate handling of the tail that would induce autotomy in wild-caught individuals. The balance of costs and benefits of autotomy is likely to diverge as males and females become sexually mature and differing social costs of tail loss for the sexes could potentially translate into different willingness to autotomize. For example, male *U. stansburiana* shed their tail significantly less willingly/easily than females, and this willingness/ease declines further as they grow older and larger (Fox, Conder & Smith, 1998). Although there is a loss in social status for both sexes, tail loss is likely to be more costly for males, as females can still retain some reproductive success in a more subordinate role. Furthermore, females autotomize a regenerated tail with the same ease as their original, while males autotomize a regenerated tail more easily, which may indicate that, for males, they have already lost social status and further tail loss may be less consequential (Fox *et al*., 1998). Cooper Jr *et al*. (2004) observed that populations of *Lacerta lilfordi* from islands with a relatively low diversity of predators often rolled and bit the callipers that were being used to induce autotomy, and latency to autotomy was much longer than that of the sister species *Lacerta hispanica* from mainland sites with a high diversity of predators that also never showed any rolling and biting behaviour. In a related taxon, the garter snake *Thamnophis sirtalis sirtalis* (Colubridae) also shows autotomy that appears to be voluntary and under central control: animals suspended by the distal tip of the tail attempt to escape by struggling and striking, and when this does not work, they rotate their bodies longitudinally in a distinctive movement and autotomize the tip of the tail (Cooper Jr & Alfieri, 1993). This example is interesting as the snakes cannot regenerate the tail tip and so are making a 'decision' that has lasting effects and presumably is based on a set of trade-offs that are assessed over a very short period of time. These data suggest that caudal autotomy is under central control, so that, to some degree, the individual can make a 'decision' about whether and when to autotomize its tail (Clause & Capaldi, 2006).

Conclusions and further research

We have addressed some of the questions raised by Arnold (1988), although in the process of preparing this paper, it became increasingly evident that the many questions he

raised are yet to be addressed with quantitative approaches, despite the intervening 20 years. Clearly, some of these questions are difficult to answer, partly because there is a complex interplay between the direct costs of losing a tail itself, the energetic burden due to losing and regrowing the tail and altered behaviour. Furthermore, these interactions are affected by sex, age and habitat. Overall, we found a great deal of evidence supporting our hypothesis that, despite similar body plans, lizards show very different inter- as well as intraspecific costs of caudal autotomy. This supports Arnold's observation that an understanding of much wider aspects of the animal is required to understand the process of autotomy. Understanding phylogeny, development, ecology and behaviour are all required to put the process of tail loss into context for each lizard species.

Generally, the literature of the past 20 years has concentrated on single questions applied to single species or populations and only a few authors have adopted a wider, comparative approach. In summary of our current knowledge, many new questions arise. Analysis of the effects of body size on autotomy incidence, for example, taking into account phylogeny would be particularly interesting ('Delicate versus more robust species'). A greater understanding of the techniques of a range of predators may be valuable in this respect ('Predation efficiency and intensity'). A greater understanding of the incidence of tail loss in response to intraspecific aggression will also be useful ('Sex differences and intraspecific aggression'). The effect of perception of danger on antipredator response is also an area that may prove profitable for future study. For example, various studies have demonstrated differences in flight initiation distances for tailless lizards ('Antipredator behaviour'), but other measures of their sensitivity to threatening situations may be valuable: interactions between perception of danger and latency to emerge from cover, locomotion speed and the 'autotomy threshold' may vary for intact or tailless individuals. Further metabolism studies would also be useful: identifying differences between the effects of tail loss and the metabolic burden of regrowing the tail have not been addressed ('Are there metabolic costs of tail loss and regrowth'). The area of lizard caudal autotomy is therefore still ripe with fascinating potential research topics. This research may continue to develop our understanding of why lizards, which have reasonably similar body forms, demonstrate such marked variability in the use and incidence of autotomy.

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