The running speed of male metallic skinks decreases by one-third after losing their tails.

A Tail of Survival

BY DAVID CHAPPLE

Tail loss is a cunning strategy that enables lizards to escape from potential predators, but how well does a lizard get by without its tail?

Lizards are remarkable escape artists, as will no doubt be obvious to anyone who has ever attempted to catch a lizard in their backyard only to be left holding a writhing detached tail.

The "voluntary" shedding of the tail might appear to be a drastic measure, but the benefit of tail loss is clear to the lizards. Dispensing with their tails enables lizards to escape the grasp of the predator, while the vigorous wriggling of the discarded appendage acts to distract the predator while the injured lizard makes its getaway.

The effectiveness of tail loss as an escape strategy is emphasised by the high incidence of tail loss in some lizard species (up to 80%). Several species have even come up with ingenious ways to improve its effectiveness. For instance, the Australian velvet gecko (*Oedura lesueurii*) waves its tail in order to encourage the predator to direct its attack towards the expendable tail.

But there are other ways to flaunt your tail. Juvenile North American broad-headed skinks (*Plestiodon laticeps*) have bright blue tails that preferentially elicit predatory attacks towards the tail. Often the shed tail even plays its part by increasing its thrashing movements when touched or bitten, to distract the would-be predator for longer.

But what happens to a lizard after it has pulled off its great escape? How does it cope without its tail? Does the absence of its tail jeopardise its subsequent survival? These are the questions that I pondered a few years ago during my Honours research at the University of Tasmania on the consequences of tail loss in the metallic skink (*Niveoscincus metallicus*).

Tail loss should definitely not be viewed as a "get out of jail free" card. To understand why it is first necessary to consider how lizards are able to lose their tails and the process of tail regeneration.

"Caudal autotomy" is the scientific term for tail loss in lizards. "Caudal" refers to the tail, while "autotomy" is the voluntary shedding of a body part (i.e. self-amputation).

Various forms of autotomy are present across the animal kingdom. For example, starfish are capable of autotomising their arms and regrowing them.

In lizards, caudal autotomy occurs in 13 of the 20 families worldwide, including four of the five lizard families in Australia (goannas are the exception). The ingenious simplicity of tail loss masks the complex adaptations that make it possible.

Caudal autotomy is made possible due to the presence of pre-existing lines of weakness through the caudal vertebrae and the surrounding soft tissue. These could be likened to perforations in paper that produce those convenient tear-off sections.

The fracture planes run through the middle of each vertebra and the adjacent muscles, nerves and blood vessels (this form of tail loss is termed "intravertebral autotomy"). This limits the soft tissue trauma that occurs during tail breaks. Astonishingly, hardly a drop of blood is spilt due to the contraction of sphincters in the caudal artery and valves in the caudal vein, which act like taps that shut off the blood flow to the shed tail region.

The lizard is far from a passive participant in the tail loss process. Intravertebral autotomy is under active neural control, and the tail can be shed without the brute physical force of the predator. ("Intervertebral autotomy" occurs when the tail is ripped off, with the break situated between rather than within the vertebrae.)

The break is generally situated 1–3 vertebrae closer to the body than where the predator grasps the lizard. This ensures that the lizard is released from the clasp of the attacker while minimising the length of tail shed.

The ability of lizards to regenerate their tails has been known since Aristotle in the 4th century BC. Not all lizard species are capable of replacing their relinquished tails, but the vast majority are.

In many species, especially skinks, the tail is longer than the rest of their body and therefore regrowing the tail represents a daunting task. For the lined rainbow skink (*Carlia jarnoldae*), the tail constitutes 12% of the total body weight.

How, then, do lizards manage to accomplish such a massive reconstruction project? Tail regeneration occurs in three distinct stages.

The first stage involves wound-healing. Despite the evolutionary steps that lizards have taken to limit the trauma incurred from discarding the tail, damage to soft tissues is inevitable. Wound-healing follows a similar process to when we get a serious cut or graze. The body gets to work repairing the damaged cells, tissues and structures. The tail stump takes on a reddish appearance due to the increased blood supply needed to fuel the repair process. A scab soon forms over the tail stump to protect the wound from the outside world and limit the potential for infection.

The second stage involves the cells at the tip of the tail stump regrouping and preparing to regrow the tail. This results in the formation of a blastema, which is an aggregation of undifferentiated stem cells that have the astonishing ability to transform into any tissue type, organ or structure.

But there is a delay of a couple of weeks before there is any visible extension of the tail. This pause before tail regrowth commences is called the "latent" period. Tail growth and extension represents the final stage of the regenerative process. The initial spurt of tail regrowth is usually rapid, but the rate gradually decreases over time.

After all of this effort, is the replacement tail as good as new? The answer is yes and no.

The new tail is definitely different. Gone are the vertebrae that made autotomy possible, replaced by a cartilaginous rod. This cartilage is less flexible than the original vertebrae, restricting the tail's range of movements.

On the plus side, the lizard does regain the ability to use its tail as a decoy during encounters with predators. But because the new section of the tail contains cartilage, subsequent tail breaks will occur closer to the body where the original vertebrae remain.

The replacement tail also looks different to the original. In some species the regenerated tail may be longer or shorter than the original. The new scales often have a different shape, colour and appearance to the original ones. So even after the entire tail has been regrown it is usually possible to see where the original tail break occurred.

Some lizard species are capable of fully regenerating their tails within 1–3 months, but other species may take a year or more to do so. This leaves the lizard in somewhat of a quandary. What does it do while it is waiting for its tail to regrow? Will the absence of the tail impede its daily life and diminish its chances of survival?

Tail loss should be viewed as a last-ditch escape mechanism. It is generally employed only after crypsis and camouflage, fleeing and other defensive measures have failed. The tail should probably have "break in case of emergency" written on it.

But tailless lizards are not able to use this strategy again until they regrow their tail. So does this reduction in the anti-predator repertoire of tailless lizards decrease their chances of surviving subsequent attacks from predators?

The answer is an emphatic yes. Staged encounters with predators in the laboratory highlight the importance of the tail to lizards. In the marbled velvet gecko (*Oedura marmorata*), only 24% of tailed lizards were successfully caught by a mammalian predator, with the remaining individuals escaping via autotomy (62%) or running (14%). In contrast, 71% of tailless lizards were captured by the predator. But does the absence of the tail alone explain the increased susceptibility of tailless lizards?

The most significant direct impact of the loss of the tail is on running speed and mobility, primarily due to its flow-on effects to almost every other aspect of daily life. During my research I found that the running speeds of male metallic skinks decreased by one-third following autotomy. In the skinks that commonly inhabit suburban gardens in eastern Australia (*Lampropholis guichenoti*), running ability is only decreased by 12–15%.

This is because the tail plays a pivotal role in lizard biomechanics. Due to its length, the tail acts as a counterbalance during running, while its lateral movement helps the lizard to maintain its momentum. The absence of the tail restricts both stride length and thrust during running.

Following tail loss a lizard has to learn how to run again, almost like an amputee completing rehabilitation. This is exemplified by the European wall lizard

The metallic skink keeps up to 75% of its fat in its tail, but most of this is kept close to the body so that only 10% of fat reserves are jettisoned when a tail is lost.

(*Podarcis muralis*), which is able to run faster after losing its tail for a second time compared with after the initial tail break.

Tailless lizards often make allowances for their decreased mobility by modifying aspects of their behaviour. Due to their decreased running speed many individuals stay closer to cover and flee sooner as a predator approaches. They might also switch to living in habitats where there are more places to hide.

But this behavioural compensation may have its own adverse consequences. Being more of a home body and becoming more wary may limit its ability to find food, decrease its territory size and social status, and reduce its mating opportunities.

Most lizard species have internal fat reserves that they rely upon to survive during harsh winters or times of severe food shortages. The fat stores literally represent energy savings that are kept for a rainy day.

But, paradoxically, most lizards store the majority of their fat in their tails. The metallic skink keeps up to 75% of its fat in its tail. Other Australian skink species (members of the *Sphenomorphus* group) have entirely abandoned the idea of keeping fat reserves in their abdomen and instead stockpile all of their energy reserves in their tail.

My research on the metallic skink revealed that this situation is not as bizarre as it initially seems. In some metallic skink populations up to 80% of individuals display the tell-tale signs of previous tail loss. So why do they store most of their energy reserves in their tail when it has a good chance of ending up on the dinner plate of a predator?

The answer is simple yet ingenious. They store almost all (90–95%) of their tail fat in the one-third of the tail that is closest to their body, yet three-quarters of all tail breaks occur in the more distant regions of the tail that lack fat stores. As a result, metallic skinks discard less than 10% of their fat reserves during autotomy. It would appear to be a small price to pay in order to escape with your life.

The direct loss of fat stores during tail autotomy appears to be minimal, but replacing a structure the size of the tail requires a substantial amount of energy and resources. A lizard's metabolic requirements may increase by 35% while it is regenerating the tail. Simply increasing the food intake is unlikely to provide the energy required to regrow the tail, and therefore it is necessary to dip into existing fat reserves.

When our families hit tough financial times we are forced to cut back on non-essential items. Similarly, following tail loss, lizards need to re-evaluate their energy budgets. This results in lizards re-directing fat reserves originally earmarked for growth or reproduction to the process of tail regeneration.

Following tail loss, female metallic skinks display a 17% decrease in the number of babies produced compared with those females that have not experienced tail loss. In the eastern water skink (*Eulamprus quoyii*) the reduction in reproductive output is as high as 75%.

Given the adversities faced by lizards following autotomy you might expect that tailless lizards would suffer a decreased likelihood of survival. This appears to be true for several species, but intriguingly not for all species. Perhaps some species have additional tricks up their sleeve to limit the costs of tail loss and enhance their chances of survival.

Intuitively, the best way to reduce the consequences of autotomy is to regrow the tail quickly. Ensuring that you cast off the minimum amount of tail in the first place means that you have less to regrow.

But it also appears that the ramifications of tail loss are related to the amount of tail lost. Chinese northern grass lizards (*Takydromus septentrionalis*) do not experience any significant reduction in their running ability until they lose more than 70% of their original tail. Conversely, Australian garden skinks regained their sprinting prowess by the time they had replaced half of their tail.

It is therefore possible that the adverse consequences of tail autotomy are less frequent and more transient in nature than traditionally believed. Lizards appear to endure some short-term pain for a long-term gain. Compared with the prospect of a grisly end in the jaws or beak of a predator, sacrificing your tail does not seem so bad.

So the next time you spot a lizard with a regenerated tail hopefully you will have a better appreciation of its amazing tale of survival.

David Chapple is an Australian Research Council (ARC) postdoctoral fellow in the herpetology section at Museum Victoria.