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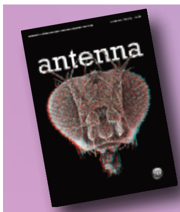

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Cover Picture: Detailed Gnat Ogre. A miniature robber fly (*Halcocephala* sp.)
Photo © Benjamin Salb (USA)

RESEARCH SPOTLIGHT

Losing a limb: autotomy and amputation in insects

> “Who would not lose a leg for such a victory?”

Henry Paget, 2nd Earl of Uxbridge, commander of 13,000 cavalry and 44 batteries of artillery at the Battle of Waterloo.

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Lord Uxbridge’s leg

On June 18th, 1815, in the closing stages of the battle of Waterloo, Lord Uxbridge’s right leg was shattered by grapeshot from opposing French artillery. Judged to be ‘completely spoiled for work’, the appendage was amputated at mid-thigh by army surgeons. Considering the circumstances, Uxbridge seems to have been relaxed about the loss of one of his four limbs. The often-quoted remark reproduced on the left indicates that Uxbridge considered that his loss was to some extent voluntary, a price to be paid for the military success of the allied cause, to which his own valour in the field had made a significant contribution. A trade-off, in other words, in which the loss was all his, while the benefit was shared with the rest of society.

Uxbridge nevertheless clearly felt that continued life would be worth living. In fact, he survived for almost another 39 years, enjoying considerable success as a politician, both in parliament and (twice) as Lord Lieutenant of Ireland. But he also recognised that there would be a price to pay in the remaining years of his life. One aspect of this was that he immediately expressed the fear that he would no longer be so attractive to the opposite sex. Displaying astonishing *sang froid* while enduring the surgeon’s knife without an anaesthetic, the injured earl joked, “I have had a pretty long run. I have been a beau these forty-seven years, and it would not be fair to cut the young men out any longer.” His concern appears to have been groundless. It is worth noting that at the time of the amputation, Uxbridge had already fathered twelve children, and he went on to sire a further four (DNB, 2008). In biological terms, his fitness remained impressive.

Aron Ralston

On April 26th, 2003, the mountaineer Aron Ralston was ill-advisedly climbing alone in Canyonlands National Park in Utah, USA. During his descent into a slot canyon, a massive boulder fell on him, crushing his right hand and pinning the arm against a rock wall. Unfortunately, Ralston had not informed anyone of his plans and had no way to call for help. After six days of this entrapment, he resolved to amputate his own arm. This required him first to break the bone by twisting the limb, and then to cut flesh and tendons with a multitool penknife as a blade. Staggering out of the canyon, he was rescued only four hours after the makeshift amputation. Ralston survived and continued mountaineering. His own description of what happened during the traumatic escape from the canyon (Ralston, 2004) and the film that was based on it have made him famous.

Insect amputees

Those two human stories raise a number of entomologically interesting questions.

It turns out that evolution recognises that it is sometimes beneficial to the individual to lose a limb, and mechanisms have evolved to facilitate this. What factors dictate which species undergo limb loss and which don't? How are insect amputations performed without tools? How is the risk of infection avoided in such amputations? Do insects amputate their own appendages? Do social insects ever perform amputations on other colony members? (The answer is yes in both cases). What are the costs and benefits of limb loss to the individual insect, and in the case of social insects, to the colony? In particular, how does having less than a full complement of appendages affect the chances of leaving offspring?

Moreover, like many other animals, but unlike humans, many insects are able to regenerate lost limbs. How widespread among hexapods is this facility? To what extent does the regenerated limb successfully replace the old one? Is regeneration closely linked to voluntary amputation? Does the ability to regenerate a lost appendage change the balance of pros and cons of choosing to lose it?

Autotomy

The equivalent process among insects to human limb amputation is the ability to voluntarily shed a limb under stress. I shall call this *autotomy,* a term that was introduced for the same purpose by Fredericq (1883). Unfortunately, since then there has been much tedious terminological dispute about this usage, involving the recommendation that use of the word 'autotomy' be restricted to situations where the limb is shed due to internal stress generated by a special muscle in the limb itself, and the invention of additional words such as 'autotilly' (used to describe limb loss due to active pulling involving other limbs) and 'autospasy' (used where another animal does the pulling).

This is unfortunate. An example of the confusion that such terminological obsession can produce is the apparent conflict between the published statements by Roth *et al.* (1984) that autotomy does not occur in spiders, because limb-shedding in arachnids is really autotilly, and the assertion by Gerald *et al.* (2017) that autotomy in spiders is very common, occurring in 5 – 40% of all individuals.

The common factor among all varieties of autotomy is that separation of the appendage from the rest of the body occurs due to adaptive structural and behavioural traits that have evolved specially for that purpose. Since we know that the ability to lose a limb has evolved on many occasions, it is not surprising that the actual mechanism employed to separate the appendage from the body varies considerably, and anyway, discovering what mechanism was used to shed a leg that has now disappeared is not easy. For these reasons, like most other modern authors, I will group all the various methods of evolved voluntary limb loss together as 'autotomy'.

Using the word in this way, many animals have the capacity to lose body parts by autotomy, with 10 out of 29 animal phyla containing species that undergo the process (Dunoyer *et al.*, 2020). It is uncertain if this means that autotomy has arisen during evolution on at least 10 separate occasions, or whether the trait has been lost on 19 occasions. Since what is meant even by the term 'limb' differs among different animal phyla; it seems to me that whether the processes of autotomic limb loss in different animal groups are really homologous is probably an unanswerable question.

Autotomy is particularly widespread in the Arthropoda, in which it appears to have been a basal character present in the phylum's earliest members (Dunoyer *et al.*, 2021) (Fig. 1). The ability to autotomise appendages has been lost, however, on a number of occasions, notably several times within the Crustacea. Loss of autotomy has also occurred in soil centipedes (Geophilomorpha) and in the Acari (mites and ticks).

> **The common factor among all varieties of autotomy is that separation of the appendage from the rest of the body occurs due to adaptive structural and behavioural traits that have evolved specially for that purpose.**

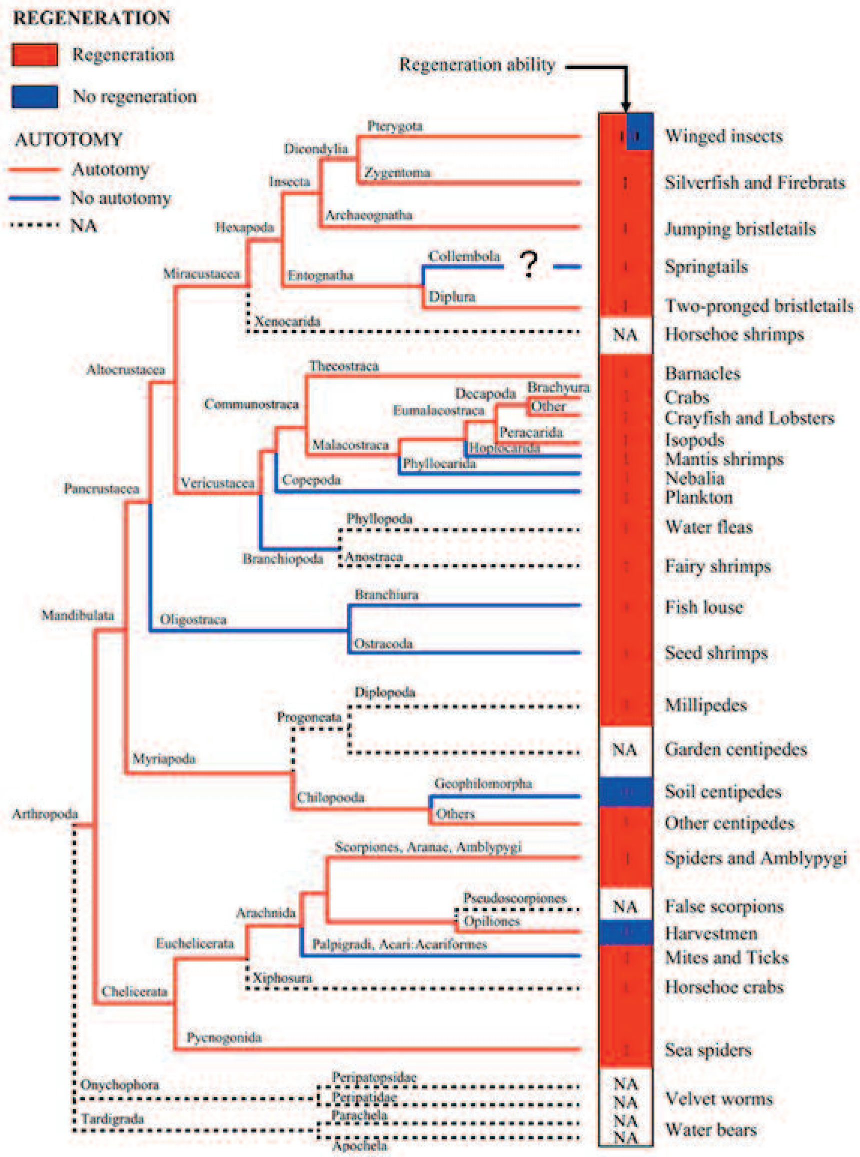


Figure 1. Evidence of regeneration and autotomy mapped onto an arthropod phylogeny. Red and blue boxes at the tips of the tree indicate presence or absence, respectively, for regeneration. Red and blue branches on the phylogeny indicate the presence or absence, respectively, of autotomy. Dashed branches indicate data are not available (NA). The question mark indicates uncertainty as to the absence of autotomy in Collembola (see text). Slightly modified from Dunoyer *et al.* (2021). Reproduced with permission.

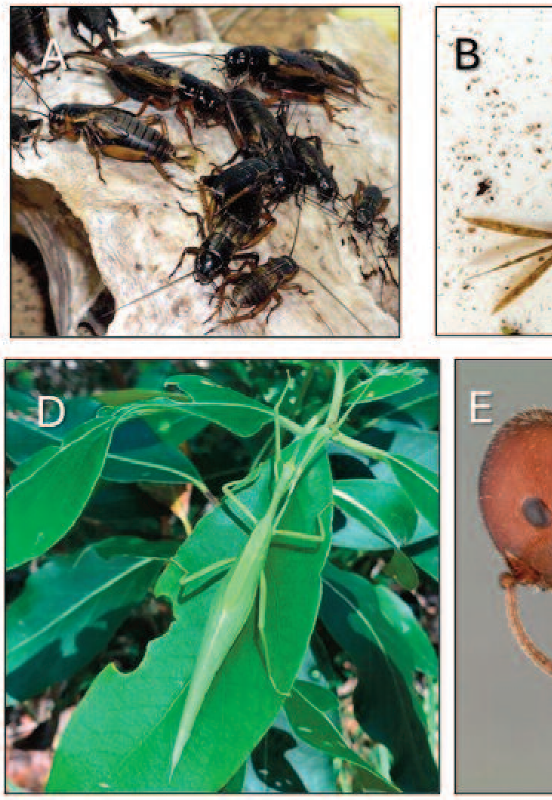
Insect autotomy

It is uncertain to what extent the voluntary shedding of legs and other appendages according to the wider definition of autotomy is possible among insects. It would be an ethically dubious project to find out by attempting to provoke it experimentally in as many species as possible. By contrast, it is relatively easy to recognise when autotomy has occurred in wild populations by looking out for absent limbs in captured insects. I suspect that almost all insects can voluntarily shed limbs, perhaps with a little help from predators, in almost all insect groups, although the specialised traits that facilitate this are most obvious in insects that don't undertake complete metamorphosis (Rolff *et al.*, 2019).

Some examples of insects that are known to readily initiate autotomy include grasshoppers and crickets (Orthoptera), mantids (Mantodea), cockroaches (Blattodea), leaf-footed bugs (Hemiptera: Coreidae and Alydidae), craneflies (Diptera: Tipulidae), as well as damselflies (Odonata: Zygoptera), which can autotomise their caudal lamellae, and honey bees (Hymenoptera: Apidae), which can autotomise their sting (Fig. 2). There is, however, no useful published list of insects that undergo autotomy; a review paper by Fleming *et al.* (2007a) lists examples of insects that can autotomise appendages of various sorts, which includes 61 species from 11 orders of insect, but the paper doesn't attempt to be exhaustive. Another review by Maruzzo *et al.* (2005) adds a few more. Actually, it would probably be more useful to catalogue those insects that are definitely known not to undergo autotomy, however extreme the provocation.

There are examples of insects that have been confirmed to undergo autotomy in every hexapod order except springtails (Collembola), and Donoyer *et al.* (2021) concluded that autotomy as a trait must have been present in the ancestral hexapod. At the same time, it should be noted that there are also examples of insects in every insect clade that apparently don't autotomise or do so only with great reluctance. Perhaps what is happening here is that insects differ in the readiness with which they voluntarily shed a limb according to the cost of the amputation.

In many insects that undergo autotomy, limbs are severed at special sites close to the trochanteral-femoral joint, where there is a preferred breakage point (PBP) or autotomy plane. An early and particularly detailed study of autotomy in phasmids, in which limb loss occurs with high frequency (Bordage, 1905),



discovered a PBP close the trochanteral-femoral articulation. This is also true of the firebrat *Thermobia domestica* (Thysanura), where leg autotomy takes place consistently at the same location. Similarly, in crickets (*Gryllus bimaculatus*), hind legs autotomise between the coxa and the trochanter, while front and middle legs also occasionally autotomise between trochanter and femur (Bateman *et al.,* 2005).

Autotomy in insects is not restricted to legs. Firebrats can also autotomise their terminal abdominal cerci, which lack specific autotomy sites but break readily at preformed lines of weakness in the integument (Buck *et al.,* 1990). The caudal lamellae ('gills') of damselfly nymphs are fragile, with a restriction in the cuticle at the base of each lamella acting as a weak point (Burnside *et al.*, 1995). Autotomising a caudal lamella when it is gripped by a predator such as a fish or a dragonfly nymph allows the damselfly to escape the predator's grasp (Gleason *et al.,* 2014). Another interesting use of autotomy on a different kind of appendage occurs in social Hymenoptera, where in a few species, once inserted into the victim, the sting undergoes autotomy and is left behind to inflict even more discomfort. The evolution of this trait will be discussed later.

Among the hexapods, as mentioned above, the only order in which the ability to undergo autotomy is said to have been completely lost is the Collembola (springtails) (Dunoyer *et al.*, 2021). I have my doubts about this because it has long been known that the antennae of the collembolan *Orchesella cincta* can regenerate after being damaged by would-be predators (Lubbock, 1873; Ernsting *et al.*, 1983). Since regeneration and autotomy are frequently linked, it would seem worthwhile to investigate this seemingly minor point again. Springtails in the genera *Orchesella* and *Tomocerus* are known to experience very high rates of antennal loss in the field (Ernsting *et al.,* 1983) raising the possibility that they have evolved to protect themselves from attack by autotomising distal antennal segments. Only a special study of antennal anatomy would resolve the point. Fig. 1 takes this reservation of mine into account.

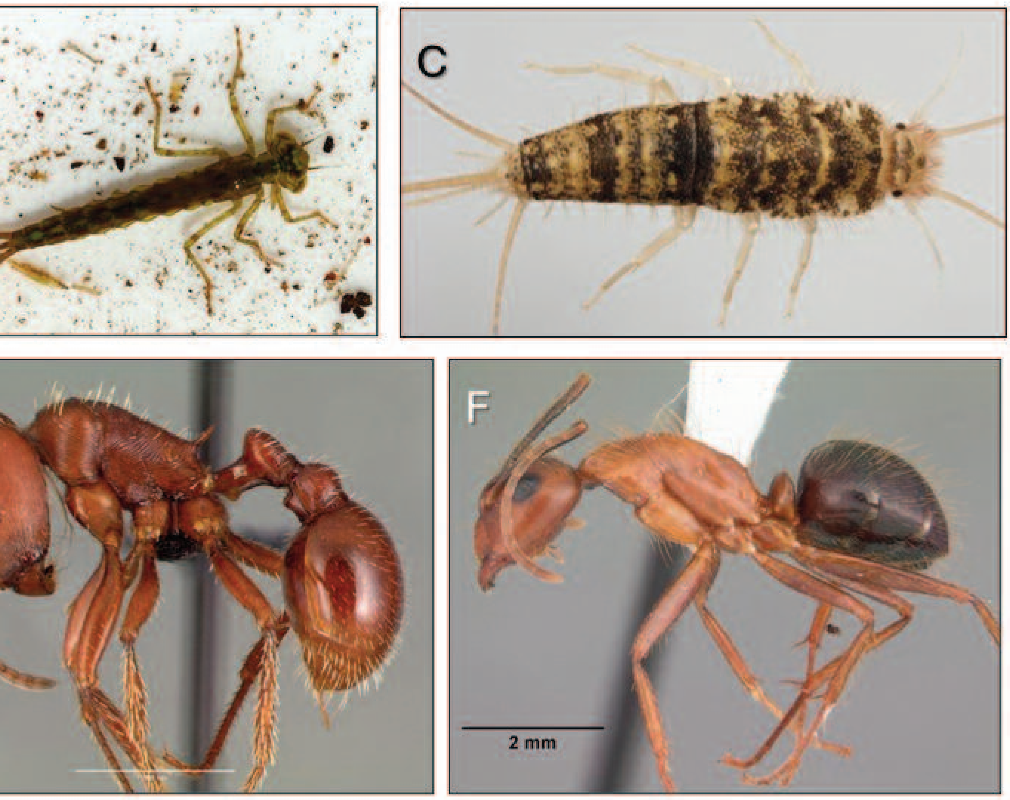


Figure 2. Images of some insects that undergo autotomy. **A.** Field crickets (*Gryllus bimaculatus*); image by Adrian Pingstone, public domain. **B.** Blue-tailed Damselfly nymph (*Ischnura elegans*); image by Charles J. Sharp, CC BY-SA 3.0. **C.** Firebrat (*Thermobia domesticus*); image by KyleCMSmth, CC BY-SA 4.0. **D.** Spur-legged Phasmid (*Didymuria violescens*); image by Jane Toner, CC BY-NC. **E.** Red Harvester Ant (*Pogonomyrmex barbatus*); image by Antweb, CC BY 4.0. **F.** Florida Carpenter Ant (*Campanotus floridanus*); image by April Nobile, CC BY 4.0.

Autotomy and regeneration

Many animals are able to regenerate lost body parts (Morgan, 1901; Seifert, 2023). Among animals in general, and notably among Crustacea and Reptilia, autotomy is closely connected with regeneration, but the reverse is not always the case. This is self-evident when considering that not all animals have appendages that can be autotomised, while some animals (*e.g.*, triclad planarians) lack limbs altogether, but nevertheless have the potential to regenerate their whole bodies from a remaining fragment. Bely *et al.* (2009) explored the phylogeny of regeneration and concluded that regeneration is more widespread than autotomy, being present in 18 of 32 animal phyla. Slack (2017) suggested that whole-body regeneration is an ancestral character which has been lost from most animal clades, while appendage regeneration "is more likely to represent a derived character resulting from many specific adaptations".

Many insects can regenerate lost appendages (see below); according to Zhong *et al.* (2023), there are hundreds of known cases, and there must be at least thousands more that have not been described. Dunoyer *et al.* (2021) compared the phylogeny of autotomy and regeneration in arthropods and reptiles. They note that in these two groups both traits have frequently been independently lost and do not easily re-evolve. While there is a clear association between autotomy and regeneration in both groups, the relationship is less strong in arthropods than it is in reptiles. I suggest that in any case this is a false comparison, since the groups that were compared are not taxonomically equivalent (phylum vs. class), and the diversity of niches occupied by the former is far wider than the latter.

There is in every animal clade a strong statistical tendency to lose regenerative ability with increasing complexity, and Elchaninov *et al.* (2021) comment, "How could such a seemingly advantageous trait as self-repair become consistently attenuated by the evolution?". These authors attribute the loss of the capacity to regenerate lost tissues to the acquisition during evolution of increasingly complicated developmentally regulated cellular signalling pathways, as well as to the progressive restriction of differentiative plasticity as a defence against cancer. It seems to me, however, that it is much more likely that the evolution of increasingly narrow niche specialisation makes it less and less worthwhile to devote resources to the regeneration of appendages that are unlikely ever to recapture the usefulness of lost limbs. Bateman *et al.* (2008) came to much the same conclusion when researching the incidence of autotomy among Orthoptera.

Where regeneration does occur, it is always associated with moulting. The extent of regeneration that can be achieved within a single moult cycle is variable between species and among appendages. In firebrats, limb autotomy is associated with the acceleration of the next moult (Buck *et al.,* 1990), while in Orthoptera the next moult is delayed (Bullière *et al.,* 1985). One might anticipate that delayed moulting would allow a greater degree of regeneration, but this does not seem to be the case (Buck *et al.,* 1990).

Autotomy and ecdysis

It is possible that autotomy, like regeneration, is ancient, having arisen even before the radiation of multicellular animals. Morgan (1901) considered regeneration to be a fundamental component of the living condition, in which case autotomy might be regarded as a subroutine of regeneration. But even if that were the case, we also know that autotomy and regeneration have both been lost in many lineages. Thus, we might still feel that it is necessary to explain why autotomy is still possible for such a wide variety of extant arthropods. One possibility is that within the Ecdysozoa, autotomy may have arisen primarily as a defence against the failure to shed the old cuticle successfully during moulting, a mishap that is almost always fatal unless immediately corrected. All arthropods moult several times, so this could explain why autotomy has been maintained as a method of escaping from entanglement in the exuviae.

Although rarely documented, the failure rate during ecdysis for most insects appears to be low; good data are rare, but Corbet (1957) found that in the field 1-2 % of emerging adult dragonflies failed to shed the old cuticle properly. But among stick insects (Phasmidae), the failure rate is much higher. According to Maginnis (2006), when phasmids are kept in captivity, approximately 30% of the insects lose a leg due to moulting complications. Of course, to some extent this might simply reflect unsuitable conditions for the captive insects, but it also indicates that moulting is potentially a big problem for these insects that can potentially be rectified by autotomising the trapped appendage. When a population of the spur-legged phasmatid *Didymuria violescens* was studied in the field in Australia, about 40% of the insects were found to have missing or regenerated legs (Maginnis *et al.*, 2007). Importantly, when predators were excluded from the field site by netting, the rate of autotomy fell by more than half to only 17.3% (Maginnis, 2008). This indicates that even in the field around 20% of individuals experience limb loss that is not the result of attempted predation, and which is probably due to failure of ecdysis followed by self-amputation. Perhaps we will soon see a new species of phasmid given the specific name *ralstoni*?

Autotomy and predation

In most cases, however, autotomy is thought to be one of the many adaptations that have arisen as a defence against predators (Sugiura, 2020; Vijendravarama, 2023). Obviously, autotomy will not help the victim much when a would-be predator is able to swallow its intended prey item whole, but when the prey insect has been seized by only a single appendage there is every chance that shedding the trapped limb will allow escape from an otherwise certain death.

Orthoptera have been much studied as examples of this straightforwardly defensive role of autotomy. Loss of limbs in wild populations is common. Bateman *et al.* (2005) found that 36% of wild-caught field crickets, *G. bimaculatus*, were missing at least one limb. When Kuriwada *et al.* (2023) captured Band-legged Ground Crickets (*Dianemobius nigrofasciatus*) in the field in Japan, they found that limb loss was variable between time and place of collection, but generally 10 – 50% of the insects had autotomised one or more limb. Autotomy was attributed to failed predation attempts, indicating that predation pressure on this species is considerable.

Clearly, if a cricket is under attack by a predator, it is better to lose a limb than to be killed. The snag, however, is that autotomy leaves the insect with one appendage less than it had before. Not surprisingly, Bateman *et al.* (2005) found that escape speed in *G. bimaculatus* that had lost a limb was reduced and that jumping ability was reduced. These consequences of autotomy will inevitably cause a direct loss of fitness for the individual in terms of reduced survival in the event of further attack by a predator.

Sex affects readiness to undergo autotomy. Although the sexual competitive ability of males that had lost two legs was not reduced, similarly handicapped females were less able to mate. The proportion of *G. bimaculatus* crickets without a limb is always higher in males than in females, which may be because males gain fitness by competing with other males to attract females; this means that males must call attention to themselves by making stridulatory calls, and so are more subject to predation. Both males and females are less willing to autotomise front legs than the other legs, presumably because both sexes use hearing organs located in front legs in order to locate singing males. Interestingly, virgin *G. bimaculatus* females are less willing to autotomise front legs than are mated females (Bateman *et al.,* 2006), and this is also true for the bush cricket *Scudderia texensis* (Tettigoniidae) (Dixon, 1989), indicating that once mated, females place lower value on their ability to listen to male mating calls.

Autotomy is only one of several defence mechanisms that can be deployed against predation. Simply being bigger may deter predators, and so it has been hypothesised that increasing size may decrease the willingness of insects to sacrifice a valuable limb through autotomy. Bateman *et al.* (2008) looked at this in Orthoptera and found that there was a significant relationship between species' average time to autotomise the limb and average body mass, with larger species demonstrating less readiness to autotomise a limb compared with smaller species. They also found, however, that those species of Orthoptera that are additionally equipped with distasteful chemical defences were much less ready to undergo autotomy than those not so defended. This makes sense, because predators need to make contact with chemically defended prey items before rejecting them.

A variation on this theme of reducing the risk of predation is the possibility of trapped insects escaping from the closing traps and adhesive hairs of carnivorous plants (Krueger *et al.*, 2023). On the other hand, according to Nentwig (1982), autotomy is unimportant as an escape mechanism for insects caught by entrapment in spiders' webs. Evidently in this case, web construction and spider responses have evolved to overcome all resistance. This may indicate that whereas it is very important to the spider to catch insects, the risk to an individual insect of being trapped in this way is small.

Autotomy-linked traits that reduce its cost

Whether escaping from a failed ecdysis, or a predator's grasp, the insect will experience greater fitness than it would have done without autotomy. Of course, the genes that will be subject to selection in this case are not limited to those that enable the act of autotomy; other genes will also be selected by predation pressure that enable autotomy-related compensatory changes in behaviour, *e.g.,* the adoption of an altered gait pattern (Fleming *et al.,* 2007b), or adopting a more cautious approach to risks from natural enemies (Stoks *et al.,* 1999). Spiders that have lost a leg alter the geometry of their webs (Vollrath, 1987). Similarly, an association may evolve between autotomy and an altered developmental pattern, *e.g.,* the onset of subsequent moults may be either delayed or accelerated, as well as the final size of the insect (Kunkel, 1977). Alternative sexual strategies may also come to be associated with autotomy, *e.g.*, a male with a reduced complement of limbs may adopt a different mating strategy as a 'sneak' rather than a mate-guarding approach (Maginnis, 2006). The role of all these traits is to mitigate the cost of autotomy, should it occur.

Like these autotomy-linked behavioural and developmental changes, regeneration is actually just another form of compensation, but it is a particularly expensive one, since the considerable resources allocated to regrowth of a lost limb cannot be used directly in support of reproduction (Prestholdt *et al*., 2022). Even with regeneration, appendage loss through autotomy is always accompanied by a net loss of fitness compared with what would otherwise have been available.

Autotomy as insurance

Some of the costs of being able to undergo autotomy must be borne even if no limbs are actually lost. This is because the structures associated with the autotomy mechanism must be in place before they can be used, and this will reduce allocation of resources to reproduction (Greenway *et al*., 2023). This means that autotomy is like a costly fitness insurance policy. The extent to which we are willing to devote resources to insurance depends on the risk of what we are insuring against, and on the hazard of the event actually occurring (Greene, 1963). As long as there is natural variation in the probability of autotomy within populations of a prey species, then an increase in the risk of predation is likely to cause an increase in investment of resources in autotomy, while the reverse will be true when the risk of predation is lower.

Damselfly nymphs are a good example of these insurance principles. These freshwater insects possess three caudal lamellae that are thin, leaf-like structures attached to the end of the abdomen by lamellar joints. Being able to shed one or more lamellae when harassed by a predator, such as a dragonfly nymph, might be advantageous to the damselfly. Presumably this is why the cuticular joints of the lamellae can be relatively easily broken when subjected to an externally applied force. But because the lamellae serve multiple functions, such as generating thrust for swimming, contributing to gas exchange, and agonistic signalling between conspecifics (Bose *et al.,* 2013) there will be a price to pay when a lamella is autotomised. Losing a lamella is known to reduce swimming speed, for example. Since fish tend to swallow damselfly nymphs whole while dragonfly nymphs are grasping predators, we would expect that lamellar autotomy would be a better defence against dragonfly nymphs than against fish.

Gleason *et al.* (2014) measured the breaking force of the lamellar joints in populations of the damselfly, *Enallagma* spp., from ponds that contained both dragonfly nymphs and fish, comparing them to those from other ponds where there were no fish (and therefore more dragonfly nymphs). The ponds with fish had damselfly nymphs with significantly higher lamellar breaking forces (*i.e.,* autotomy was less likely). This is consistent with dragonfly larvae exerting a selective pressure in favour of autotomy.

Autotomy is like a costly fitness insurance policy

Sting autotomy

Social Hymenoptera workers have a modified ovipositor that acts as a defensive sting. The anatomy of the sting apparatus is very similar across all social wasps (Snodgrass, 1910; Mulfinger *et al*., 1992; Ramirez-Esquivel & Ravi, 2023) but the workers of a few species of wasps and bees that behave aggressively towards large vertebrates, highly dangerous potential enemies near their nests, have specially adapted stingers that allow the self-amputation of the stinger and poison sac, or sting autotomy. This occurs in Honey Bees (*Apis mellifera*), harvester ants (*Pogonomyrmex* spp.) and certain tropical wasps from the tribes Epiponini, Polistini, and Ropalidiini (Hermann, 1971; Sledge *et al*., 1999). These bees and wasps are all characterised by a well-developed and highly barbed sting lancet (Bissessarsingh *et al.,* 2021).

Upon insertion of the sting lancet into the victim, its barbs lock into the tissue, then muscles at the end of the abdomen contract, releasing venom into the wound. Relaxation of the supporting muscles facilitates the separation of the whole stinging apparatus from the rest of the abdomen upon pulling away of the stinging insect (Hermann, 1971). Species that exhibit sting autotomy have muscles that will easily tear from the internal structures, while species without autotomy have well-developed abdominal muscles that prevent this separation (Manzoli-Palma *et al*., 1997). Sting autotomy has also sometimes been observed to occur in human sting victims of the vespulid wasps *Vespula maculifrons* and *Vespula flavopilosa,* but this occurs only rarely (Mulfinger *et al*., 1992) because these wasps lack the specialised lancet and muscle adaptations that promote sting autotomy.

Wing shedding in ant queens

Independent colony foundation by ants is performed by winged queens that disperse by flight, mate and found their colony alone (Hölldobler *et al*., 1990). Having completed her nuptial mating flight, the queen sheds her wings, which are no longer needed for flight, and the energy and nutrients from the wing muscles can be used to build the new colony and produce the first brood of workers (Peeters *et al.,* 2001). This doesn't happen in honey bees, which need to keep their wings for swarming, or in bumblebees, where the queen may need them for foraging.

The queen ant's loss of her wings can be considered to be autotomy, in the sense that it is an evolved, voluntary loss of a body part. There are, however, no special anatomical adaptations of the wings, and in most species the newly mated queen simply bites or pulls the wings at their bases to remove them. The advantage of wing shedding is usually supposed to be that the queen will no longer need her wings once a nest has been started, and it is easier for her to move around in the nest if they are no longer attached, but I don't know of any evidence to support the latter assertion.

Perhaps more important from the point of view of fitness, the queen's thoracic flight muscles now also degenerate, and the materials and energy thus released are reallocated to reproduction (Jones *et al.,* 1978). Despite the long life still ahead of her, the queen will not moult again, so there can be no regeneration of either the wings or the muscles. There is no cost to the queen's fitness, only a small gain that is nevertheless conferred at a crucial time in the colony's development, so this characteristic behaviour may be expected to persist.

Infection: the disposable individual vs medical treatment

There is evidence that in some animals autotomy can be used as a way of eliminating parasites from the body. For example, Bilej *et al.* (2000) hypothesised that earthworms can eliminate coelomic parasite infections by encapsulating the offending organisms and then disposing of them through autotomy of the caudal region of the body (although Keilin (1925) supposed that the same phenomenon was under the control of the parasite and was a method whereby parasite propagules could be liberated into the environment). Mitoh & Yusa (2021) have drawn attention to the 'extreme autotomy' undergone by sacoglossan sea slugs (Mollusca: Gastropoda), which eliminate copepod parasites by shedding and then regenerating a large proportion of their body, including the heart. It's true that regenerating the autotomised tissues will be expensive in terms of resources acquired in the future, but without autotomy there might be no future and no fitness at all.

As far as I know, no arthropod experiences such extreme autotomy, but there are certainly examples where some social insects reduce the risk of infection through altruistic self-sacrifice of whole insects. In colonies of ants, bees and wasps, infection is most likely to be introduced by workers returning from foraging trips outside the nest. This is potentially highly dangerous to the colony (Loreto & Hughes, 2016). In order to avert this danger, workers which are individually infected with transmissible parasites or pathogens may voluntarily fail to return to the nest (Tofilski *et al*., 2008), or are actively killed by other colony members, which dispose of the body outside the nest (Cremer *et al.,* 2019). Both individual self-sacrificial behaviour and sibling murder are favoured by natural selection because although it is lethal to individual workers, it protects the queen's fitness and, by extension, the worker's own inclusive fitness (Hamilton, 1963; Bourke, 2009). In this way a defensive role is ascribed to the 'disposable individual' (Aanen, 2018). I will not go so far as to call this murderous defensive behaviour an example of autotomy, but I hope that you can see that it is at least analogous.

There is an alternative to the 'disposable individual' defensive strategy in which other members of the ant colony exhibit colony level 'rescue behaviour' towards nestmates that are in trouble. One example of this is displayed by the Mediterranean formicine ant *Cataglyphis piliscapa*, in which one or more nestmates attempt to free a physically entrapped nestmate (Hollis *et al*., 2022). In an elaboration of such behaviour, workers of the ponerine ant *Megaponera analis* will rescue nestmate workers that have been physically injured. *Megaponera* *analis* is a specialist predator of termites, and raids on termite nests frequently result in injuries to the raiding ants. While severely damaged ants are left to die, workers with less serious injuries are transported back to the home nest, where they are given restorative care. Most rescued ants were able to resume raiding within days (Frank *et al.*, 2017). The treatment given to the injured ants (Frank *et al.*, 2023) involves active cleaning ('allogrooming') of the body surface and application of antimicrobial secretions from their own metapleural glands; this reduces mortality among the rescued ants by 90%. In ants like these, we see that the emphasis is not on preserving the society at the expense of individual members, but on maximising the colony's inclusive fitness through medical intervention in the fate of individual colony members. Frank *et al.* (2017) constructed a mathematical model which estimates that rescue behaviour enables colonies of *M. analis* to maintain ant populations that are 29% larger than would otherwise be the case. They point out that rescue behaviour of this type can only evolve where the benefit to the colony exceeds the cost of the rescue. This means that it is most likely to occur in group-hunting species, where an injured ant can easily be detected by its nestmates, and where all the raiding ants return together to the nest. It also requires that the rescuing ants produce adequate quantities of antimicrobial secretions to be used in the medical treatment of rescued nestmates.

Social amputation in ants

But in some formicine ant genera, including carpenter ants (*Camponotus* spp.) the metapleural glands have been lost, meaning that much of the fitness benefit to be derived from the 'medical care' option is unavailable to these ants. Despite this, these ants continue to follow the 'rescue' model rather than the 'disposable ant' model.

Frank *et al.* (2024) discovered that in certain circumstances, *C. floridanus* workers provide surgical care to injured nestmates by amputating an injured limb. In these experiments, worker ants were experimentally injured at the level of the femur. The wound was either sterile, or was infected with *Pseudomonas aeruginosa*, a Gram-negative bacterium that is a lethal pathogen in *C. floridanus*. Once injured and/or infected, the experimental workers were either returned to the nest or remained in isolation.

Among those ants returned to the nest, almost 90% of the injured-infected ants were rapidly (< 1.5 h) assessed by their nestmates and then subjected by them to amputation of the affected leg at the level of the trochanter (Fig. 3). Ants that had been infected and then experimentally amputated at the same leg position were also returned to the nest, but received little attention from nestmates and did not experience further attempted amputations. Whether the infected leg was removed by nestmates or experimenters, amputation was highly effective in preventing the proliferation of bacteria in the treated insects. As a result, survival of amputated insects, with or without infection, was the same as in untreated controls. By comparison, those insects that had been infected and were returned to isolated conditions (*i.e.*, they did not

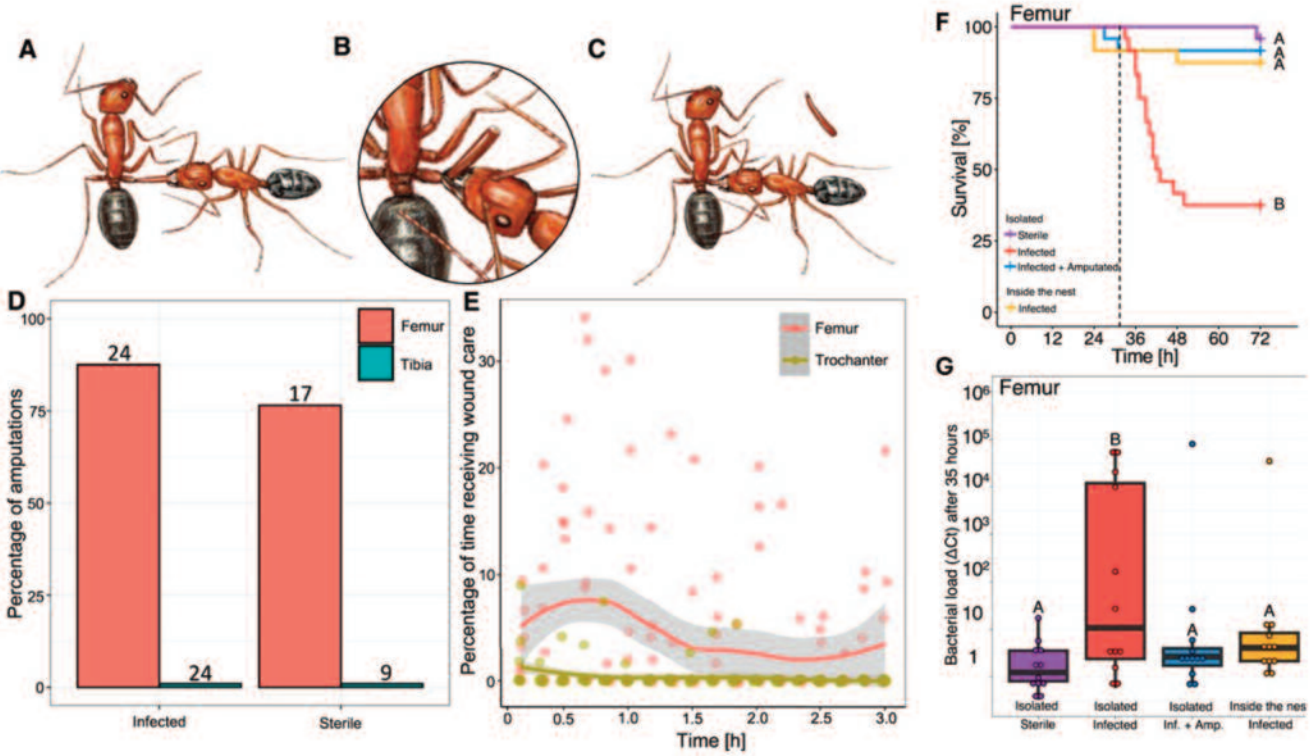


Figure 3. Amputation and wound care behaviour in *C. floridanus*. **A.** Worker providing wound care on a femur-injured individual. **B.** Worker amputating (biting) the injured leg at the trochanter. **C.** Worker providing wound care on newly created trochanter wound after amputation. **D.** Percentage of amputations performed on ants with an infected or sterile femur (red) or tibia (blue) injury after 24 h; numbers represent the sample size. **E.** Percentage of time injured ant received wound care behaviour over 3 h; Line is polynomial regression with 95% confidence interval for the first 3 h after the experimental femur injury (femur, red: $n = 8$) and the first 3 h after amputation on the trochanter wound (trochanter, brown: $n = 7$). **F.** Cumulative survival rates of femur-injured ants over 72 h. **G.** Boxplots showing bacterial load in ant bodies after removal of the gaster; significant differences ($P < 0.05$) are shown with different letters. Reproduced from Frank *et al.* (2024), CC-BY licence.

receive care or amputation from nestmates) fared badly, experiencing bacterial proliferation and more than half of them died within 48 hours.

As in the case of the hero of Waterloo, but unlike Ralston, amputation in *Campanotus* is performed by others rather than being self-inflicted. As far as we know, like both the Earl of Uxbridge and Aron Ralston, the injured ants experience limb removal without the benefit of an anaesthetic. But unlike both humans, the ants benefit from the application of antibiotic secretions at the time of amputation that effectively prevent infection by environmental bacteria. As Frank *et al.* (2024) point out, these experiments indicate that *Campanotus* ants invented surgical amputation millions of years before the equivalent procedure was invented by humans.

Ants invented surgical amputation millions of years before the equivalent procedure was invented by humans.

References

Aaanen, D.K. (2018) *Current Biology* **28**, R306–R327.
Bateman, P.W. *et al.* (2005) *Animal Behaviour* **69**, 151–159.
Bateman, P.W. *et al.* (2006) *Biology Letters* **2**, 33–35.
Bateman, P.W. *et al.* (2008) *Journal of Orthoptera Research* **17**, 315–320.
Bely, A.E. *et al.* (2009) *Trends in Ecology and Evolution* **25**, 161–170.
Bilej, M. *et al.* (2000). *Folia Microbiologica* **45**, 283–300.
Bissessarsingh, M. *et al.* (2021) *Insects* **12**, 729.
Bordage, E. (1905) *Bulletin Scientifique de la France et de la Belgique* **39**, 307–454.
Bose, A.P.H. *et al.* (2013) *Evolutionary Ecology* **27**, 27–38.
Bourke, A.F.G. (2009) *Principles of Social Evolution*. Oxford University Press, Oxford (UK).
Buck, C. *et al.* (1990) *Journal of Experimental Biology* **151**, 341–347.
Bullière, F. *et al.* (1985) In: Kerkut, G.A. *et al.* (eds) *Comprehensive Insect Physiology, Biochemistry and Pharmacology*, vol. 2. Pergamon Press, Oxford (UK), pp. 371–424.
Burnside, C.A. *et al.* (1995) *Zoological Journal of the Linnean Society* **114**, 155–171.
Corbet, P.S. (1957) *Journal of Animal Ecology* **26**, 1–69.
Cremer, S. *et al.* (2007) *Current Biology* **17**, R693–702.
Dixon, K. (1989) *Canadian Journal of Zoology* **67**, 1607–1609.
DNB (2008) *Dictionary of National Biography*. https://doi.org/10.1093/ref:odnb/21112
Dunoyer, L.A. *et al.* (2021) *Journal of Experimental Zoology Part B* **336**, 94–115.
Elchaninov, A. *et al.* (2021) *Frontiers in Ecology and Evolution* **9**, 621686.
Ernsting, G. *et al.* (1983) *Netherlands Journal of Zoology* **33**, 476–484.
Fleming, P.A. *et al.* (2007a) *Biological Reviews* **82**, 481–510.
Fleming, P.A. *et al.* (2007b) *Journal of Experimental Biology* **210**, 1446–1454.
Frank, E.T. *et al.* (2017) *Science Advances* **3**, e1602187.
Frank, E.T. *et al.* (2023) *Nature Communications* **14**, 8446.
Frank, E.T. *et al.* (2024) *Current Biology* **34**, 3273–3278.
Fredericq, L. (1883) *Archives de zoologie expérimentale et Générale* **2,** 413–426.
Gerald, G.W. *et al.* (2017) *Ecology and Evolution* **7**, 6729–6735.
Gleason, J.E. *et al.* (2014) *Journal of Experimental Biology* **217**, 185–191.
Greene, M.R. (1963) *Journal of Insurance* **30**, 165–182.
Greenway, E.V. *et al.* (2023) *Evolution* **77**, 1422–1429.
Hamilton, W.D. (1963) *American Naturalist* **97**, 354–356.
Hermann, H.R. (1971) *Insectes Sociaux* **18**, 111–120.
Hölldobler, B. *et al.* (1990) *The Ants*. Harvard University Press, Cambridge, Massachusetts (USA).
Hollis, K.L. *et al.* (2022) *Learning and Behavior* **50**, 329–338.
Jones, R.G. *et al.* (1978) *American Journal of Anatomy* **151**, 603–610.
Keilin, D. (1925) *Parasitology* **17**, 170–172.
Krueger, T. *et al.* (2023) *Arthropod-Plant Interactions* **17**, 593–599.
Kunkel, J.G. (1977) *Biological Bulletin* **153**, 145–162.
Kuriwada, T. *et al.* (2023) *Behaviour* **160**, 337–355.
Loreto, R.G. & Hughes, D.P. (2016) *PLoS ONE* **11**, e0160820.
Lubbock, J. (1873) *Monograph of the Collembola and Thysanura*. Ray Society, London.
Maginnis, T.L. (2006) *Behavioral Ecology* **17**, 857–872.
Maginnis, T.L *et al.* (2007) *Australian Entomologist* **34**, 27–32.
Maginnis, T.L. (2008) *Florida Entomologist* **91**, 126–127.
Manzoli-Palma, M.D. *et al.* (1997) *Journal of Advanced Zoology* **18**, 1–6.
Maruzzo, D. *et al.* (2005) Appendage loss and regeneration in arthropods: A comparative view. In: Koenemann S. *et al.* (eds.) *Crustacea and arthropod relationships*. CRC Press, Boca Raton, pp. 215–246.
Mitoh, S. & Yusa, Y. (2021) *Current Biology* **31**, R233–R234.
Morgan, T.H. (1901) *Regeneration*. The Macmillan Company, New York. https://archive.org/details/regeneration00morggoog
Mulfinger, L. *et al.* (1992) *Journal of Medical Entomology* **29**, 325–328.
Nentwig, W. (1982) *Oecologia* **53**, 412–441.
Peeters, C. *et al.* (2001) *Annual Review of Entomology* **46**, 601–630.
Prestholdt, T. *et al.* (2022) *Behavioral Ecology* **33**, 518–525.
Ralston, A. (2004) *Between a Rock and a Hard Place*. Simon and Schuster UK, London (UK).
Ramirez-Esquivel, F. & Ravi, S. (2023) *iScience* **26**, 107103.
Rolff, J. *et al.* (2019) *Philosophical Transactions of the Royal Society B* **374**, 20190063.
Roth, V.D. *et al.* (1984) *Bulletin of the British Arachnological Society* **6**, 137–146.
Seifert, A.W. (2023) *Communications Biology* **6**, 1139.
Slack, J.M.W. (2017) *EMBO Reports* **18**, 1497–1508.
Sledge, M.F. *et al.* (1999) *Physiological Entomology* **24**, 234–239.
Snodgrass, R.E. (1910) *The anatomy of the honey bee*. US Bureau of Entomology, Washington D.C. (USA).
Stoks, R. *et al.* (1999) *Behavioral Ecology and Sociobiology* **47**, 70–75.
Sugiura, S. (2020) *Entomological Science* **23**, 316–337.
Tofilski, A. *et al.* (2008) *American Naturalist* **172**, E239–E243.
Vijendravarama, R.K. (2023) *Journal of Evolutionary Biology* **36**, 967–974.
Vollrath, F. (1987) *Nature* **328**, 247–248.
Zhong, J. *et al.* (2023) *Cell Regeneration* **12**, 9.

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