



# Better to risk limb than life: some insects use autotomy to escape passive predation by carnivorous plants

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Received: 29 March 2023 / Accepted: 12 May 2023 / Published online: 30 May 2023  
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## Abstract

Limb autotomy, the voluntary shedding of body parts as a strategy to escape predation or entrapment, is particularly common in insects and other arthropods that are frequently captured by the carnivorous plant genus *Drosera*. However, no study has previously examined the effectiveness of autotomy at facilitating escape from these passive, sessile plant predators. Using field observations of numerous *Drosera* species in Western Australia and Australia's Northern Territory, we present the first field evidence of limb autotomy being employed by insects and other arthropods to escape capture by carnivorous plants. Most autotomised limbs found on the *Drosera* traps belonged to large nematoceran flies, probably comprised primarily of Tipulidae (crane flies), which have a characteristically large, slender body with very long limbs that seems likely to allow the effective use of autotomy as a strategy to prevent fatal capture. However, autotomy was overall only rarely observed amongst the *Drosera* prey as most prey items were small and quickly became completely enveloped by the sticky mucilage, rendering any such escape attempts impossible. Finally, we determined that the likelihood of escape decreased markedly as multiple limbs were lost.

**Keywords** *Drosera* · Sundews · Tipulidae · Crane flies · DNA metabarcoding

## Introduction

Autotomy, the voluntary shedding of body parts (Frédéricq 1883), has evolved in multiple lineages of animals, typically in response to predation (Emberts et al. 2020). Many taxa of invertebrates are able to autotomise a wide range

of body parts, usually along a pre-formed breakage plane (Fleming et al. 2007). Autotomy is particularly common in insects and other arthropods, where the process most frequently involves the voluntary shedding of limbs to escape predation or entrapment (Fleming et al. 2007; Emberts et al. 2016). Autotomy of limbs allows immediate escape from predation where the limb or limbs in question have been gripped or trapped in some manner by a predator. However, it incurs potential costs to locomotion, feeding, and thus reproduction, and may compromise future escape from predation (Bateman and Fleming 2005, 2006; Fleming and Bateman 2007).

Limb autotomy can occur rapidly (i.e. < 2 min sensu Emberts et al. 2020) in many species of insects and other arthropods, and this rapidity is expected to be crucial to successful escape from animal predators (Emberts et al. 2020; Fleming et al. 2007). It is likely that for many insect lineages rapid autotomy has evolved from slow autotomy, where the process of limb shedding often takes > 20 min (Emberts et al. 2020). Slow autotomy is hypothesised to have evolved as a mechanism to reduce the cost of injury (i.e. by autotomising injured limbs that hinder movement) or to escape from non-predatory entanglement of limbs, such as can

Handling Editor: Dagmar Voigt.

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occur during moulting (Emberts et al. 2016). For example, the contemporary rapid limb autotomy for escaping predation exhibited by leaf-footed bugs (Hemiptera: Coreidae and Alydidae) appears to have evolved from an ancestral slow autotomy state employed for escape from non-predatory entrapment (Emberts et al. 2020). However, there is at least one situation where slow autotomy likely still represents an effective predatory escape mechanism: where an individual has been captured by a passive, sessile predator and the processes causing mortality are prolonged.

Sticky glandular trichomes evolved multiple times in angiosperms, mainly for herbivore defence, and can be found in more than 110 plant genera from 49 botanical families (LoPresti et al. 2015). Plant carnivory evolved at least 10 times independently in angiosperms, in most cases from glandular sticky ancestors (Fleischmann et al. 2018a). Out of the many carnivorous trap types, adhesive traps are realised in seven extant carnivorous plant genera from seven different families in three angiosperm orders (Fleischmann et al. 2018a), the sundews (*Drosera* L., Droseraceae) being the largest genus of sticky carnivorous plants with about 260 species currently recognised (Fleischmann et al. 2018b; Krueger et al. 2023). *Drosera* deploy leaves possessing stalked glands (tentacles) that secrete a highly viscous, water-based mucilage, and proteolytic enzymes to capture and digest prey, with both leaves and tentacles often capable of significant movement to maximise the contact of this mucilage with captured organisms (Darwin 1875; Juniper et al. 1989). Mortality in prey captured by *Drosera* usually is not immediate as death typically results from asphyxiation or exhaustion after several minutes to hours (Juniper et al. 1989) or ongoing release of proteolytic enzymes during prey digestion which commences about 30 min after initial capture by most adhesive carnivorous plants (Heslop-Harrison 1975). Many *Drosera* rely upon the struggle of captured prey to stimulate tentacle movement and to maximise mucilage coverage (Darwin 1875; Williams 1976; Krausko et al. 2017; Poppinga et al. 2018). Larger prey body size and more prey movement cause faster and stronger tentacle reactions and leaf bending of *Drosera* traps (Darwin 1875; Williams 1976).

*Drosera* can be highly effective passive predators, with large-leaved species often capturing dozens of prey on single leaves, and most frequently capture small insects and arthropods from orders, including Diptera, Hemiptera, Hymenoptera, Lepidoptera, Thysanoptera, Coleoptera, Orthoptera, Collembola, and Araneae (studies from Western Australia: Watson et al. 1982; Verbeek and Boasson 1993; Krueger et al. 2020, 2022). Many species within these orders are known to utilise either slow or rapid limb autotomy (Fleming et al. 2007). The mucilage-laden *Drosera* tentacles have a moderate retention potential on captured prey (Watson et al. 1982; Gibson 1991; Murza et al. 2006); however with

tentacle movement and leaf bending, prey is more firmly secured on the leaf (Darwin 1875; Poppinga et al. 2018). At the early stages of the trapping process, differential escape of prey from *Drosera* leaves is possible, when the captured insect is large and strong enough to pull itself off the sticky trap (Gibson 1991) or is able to autotomize the stuck extremities (Cross and Bateman 2018). We hypothesise that any insect or arthropod capable of limb autotomy that becomes entrapped by *Drosera* may potentially facilitate escape by shedding the entrapped limb(s). In a controlled laboratory experiment it has been shown that crickets (*Acheta domesticus* L.; Orthoptera, Grillidae) that had already undergone a single-hind limb autotomy were less able to escape from *Drosera collina* (N.G. Marchant & Lowrie) Lowrie (*D.* subgenus *Ergaleium*) leaves than were intact individuals of the same size class—this escape ability further declined with the loss of the second hind limb (Cross and Bateman 2018). However, no study has previously examined the incidence of limb autotomy by insects or arthropods captured by *Drosera* or other adhesive-trapped carnivorous plants under natural conditions and thus it remains unknown to what extent this strategy is effective at facilitating their escape from these passive, sessile plant predators.

Here, we present the first examination of limb autotomy by insects or other arthropods captured by carnivorous plants. We determined the incidence and identified the source of autotomised limbs found on *Drosera* from *D.* section *Arachnopus* (a group of annual species known as the “*Drosera indica* complex”) from northern Australia. The 13 currently described species from this section all have an erect growth habit, producing narrowly linear-lanceolate trapping leaves (Lowrie 2014; Krueger and Fleischmann 2021; Krueger et al. 2022), and the prey spectra (i.e. the number and composition of captured prey) of several species have been well studied recently (Krueger et al. 2020, 2022). We further examined and identified autotomised limbs on the trapping leaves of eight species of the morphologically extremely diverse *D.* section *Ergaleium* (tuberous sundews) and of four species of *D.* section *Bryastrum* (pygmy sundews), occurring in southwest Western Australia. We aimed to (a) determine whether limb autotomy was employed as a strategy by insects and arthropods to escape capture by *Drosera*; (b) identify which insect and arthropod groups employed limb autotomy to escape *Drosera*, if the strategy was employed; and (c) evaluate if the escape likelihood increases or decreases with the number of limbs lost.

## Methods

In situ photographs of the leaves of ca. 150 *Drosera* species from Western Australia (South-West and tropical North) and the Northern Territory, taken between 2008 and 2022, were

examined for autotomised limbs. Photographs were captured using a Panasonic Lumix G81 (Panasonic, Osaka, Japan) with a Panasonic Lumix G Macro 30 mm f/2.8 ASPH lens (Panasonic, Osaka, Japan) or a Nikon D5100 DSLR (Nikon, Tokyo, Japan) with standard lenses and Raynox DCR-150 or DCR-250 macro adapters (Raynox, Tokyo, Japan). In total, ca. 91,000 photographs were examined, including the 15,693 photographs used in the prey spectra study of Krueger et al. (2020). Ca. 70% of all leaves with observed autotomised limbs were photographed from multiple angles to maximise the amount of discernible morphological features (Krueger et al. 2020, 2022). Previous studies have shown such photographic analysis of *Drosera* prey to be accurate at coarse taxonomic resolution, efficient, and non-destructive (Krueger et al. 2020, 2022). In total, 45 of the 80 observed cases of limb autotomy were observed using the systematic photography approaches of Krueger et al. (2020, 2022), the remainder of the cases were observed in photographs that were captured of *Drosera* plants during field studies and surveys. For some autotomised limbs sampled during 2019 and 2020 and 2022, DNA metabarcoding was employed to obtain a finer taxonomic resolution following photographic examination (methodology following Krueger et al. 2022).

For each instance of observed autotomy, the number of autotomised legs or wings was counted, and the successful (or unsuccessful) escape of the captured prey was determined by the absence (or presence) of the limb donor on the trapping leaf. Similar sized and shaped legs found in close proximity on a single *Drosera* leaf were treated as one case of autotomy, whilst legs found on different leaves of the same plant were treated as multiple cases of autotomy unless the limb donor was present (i.e. the escape attempt was unsuccessful). In the latter case, the number of autotomised legs found on nearby leaves of the same plant was compared against the number of missing legs on the limb donor to determine if one or multiple cases of autotomy took place on the plant.

Binary logistic regression (SPSS Statistics 28, IBM) was employed to examine whether success of escape following limb autotomy was predicted by the number of limbs lost. Regression was undertaken using all cases to explore for a global trend and additionally for large nematoceran fly cases as a case study of a single prey group, given that this arthropod family represented the majority of autotomy cases.

## Results

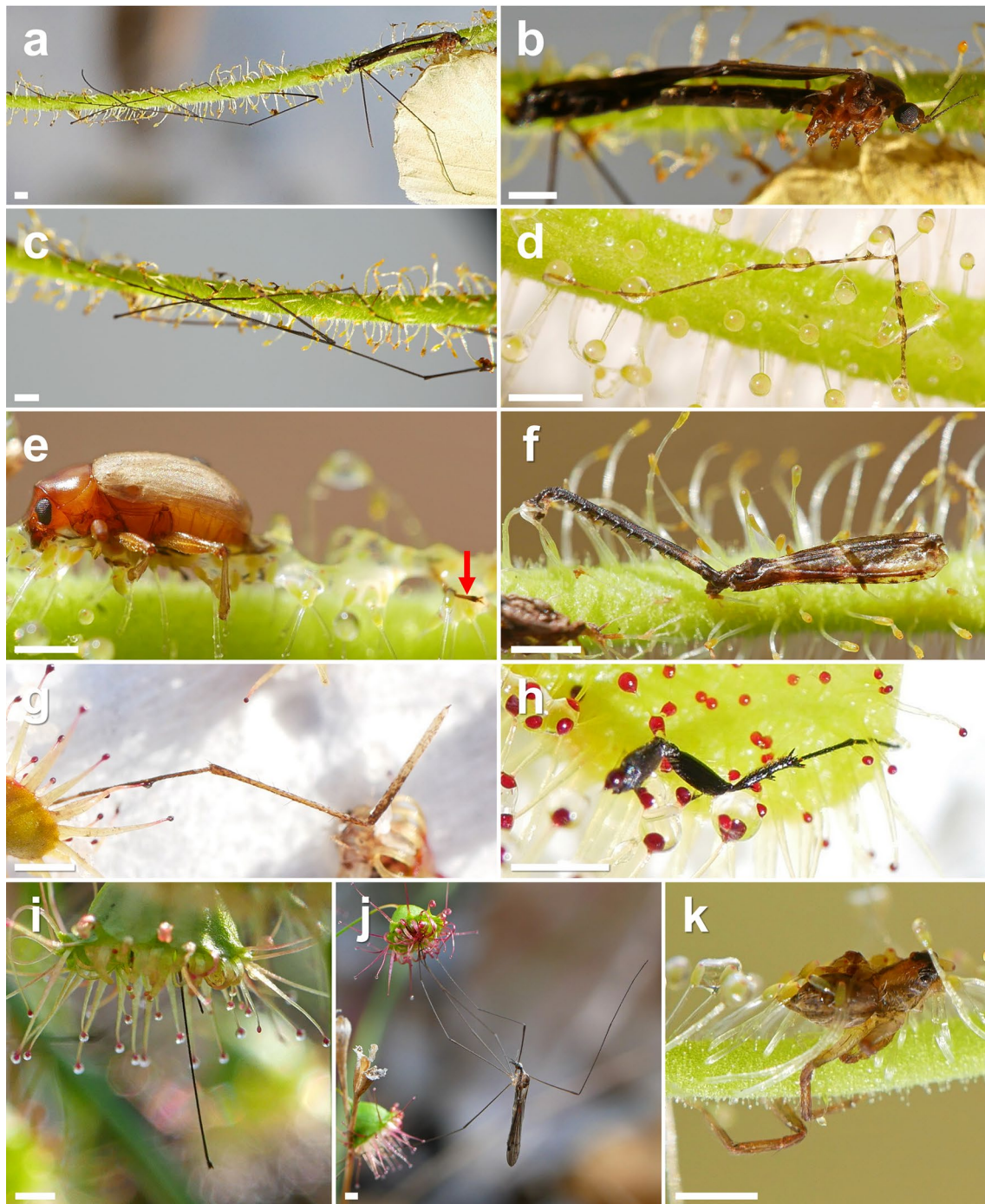
Photographic analysis found 80 instances of limb loss likely resulting from autotomy, comprising 168 total limbs on individuals from 21 different species of *Drosera*, belonging to four sections (Online Resource 1, Fig. 1). Autotomised limbs were observed on the large, narrowly linear-lanceolate leaves

of almost all *Drosera* from section *Arachnopus* occurring at 17 different locations in the monsoon tropical Kimberley and Top End regions of Western Australia and the Northern Territory (*D. aff. glabriscapa*, *D. aff. serpens*, *D. aquatica*, *D. aurantiaca*, *D. barrettiorum*, *D. cucullata*, *D. finlaysoniana*, *D. fragrans*, *D. hartmeyerorum*, *D. margaritacea*, *D. nana*, and *D. serpens*; Online Resource 1). Several examples of potential autotomy were also observed at eight different locations in the subtropical Southwest Australian Floristic Region (which has a Mediterranean climate): on six members of *D. section Ergaleium* (*D. collina*, a species with large, flat leaves and others with much smaller roundish, more or less peltate trap leaves: *D. huegelii*, *D. rupicola*, *D. salina*, *D. stolonifera*, *D. stricticaulis*, and *D. zigzagia*) and on one species of *D. section Bryastrum* (*D. gibsonii*, which likewise has very small, roundish leaves). A single case of an autotomised limb was also found on one species of *D. section Lasiocephala* from the Northern Territory (*D. ordensis*, a species with small- to medium-sized roundish traps).

Examination suggested that autotomy may have facilitated escape in 29 cases (36%) of recorded limb autotomy, but was unsuccessful (i.e. the limb donor remained captured elsewhere on the leaf) in the other 51 cases (64%). The number of limbs present for each discrete instance of autotomy ranged from one to six (mean  $2 \pm 0.1$ ), with lower numbers being much more common (Fig. 2). Only in one case was the apparent loss of all six legs observed (Figs. 1a–c, 2).

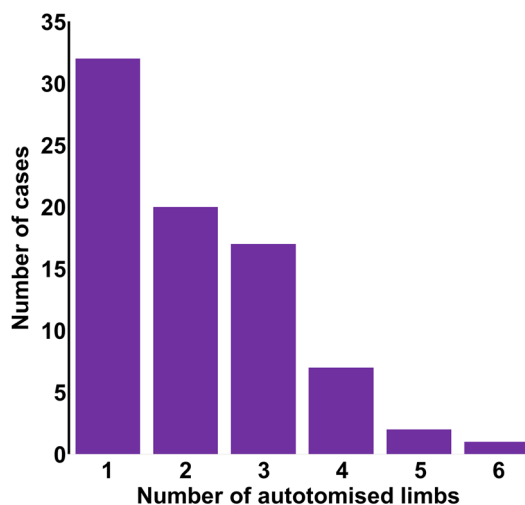
Considering all cases, the likelihood of autotomy facilitating successful escape from *Drosera* decreased by 45% with each additional limb lost ( $\text{Exp}(B) = 0.446$ ,  $\chi^2 = 8.702$ , d.f. = 1,  $P = 0.003$ ). Considering only large nematoceran fly cases, the loss of each additional limb reduced escape likelihood by 46% ( $\text{Exp}(B) = 0.455$ ,  $\chi^2 = 7.029$ , d.f. = 1,  $P = 0.008$ ).

Autotomised limbs primarily belonged to large nematoceran flies (Diptera) and probably comprised mainly of the family Tipulidae (crane flies, 83% of all cases including one barcoded to the species *Symplecta pilipes* Fab.; Online Resource 1, Fig. 1a–c, i, j). Additional nematoceran limbs were identified as the genus *Dilophus* (Bibionidae; Fig. 1h), Cecidomyiidae, and Culicidae (including a species of *Anopheles* and one barcoded to *Aedes camptorhynchus* Thomson; Fig. 1g). Additional limbs were identified from representatives of Araneae (spiders; Fig. 1k), Coleoptera (beetles, barcoded to Chrysomelidae; Fig. 1e), Hemiptera (true bugs, identified as a species of *Setocoris*), Lepidoptera (moths and butterflies, morphologically identified as a species of *Utetheisa*), and Orthoptera (crickets; Fig. 1f). Three limbs could not be identified to arthropod order.



**Fig. 1** Examples of limb autotomy in *Drosera* prey from Western Australia. **a–c** Tipulidae flies (Diptera) captured by *D. cucullata* (*D.* section *Arachnopus*) with all limbs autotomised; **d** autotomised limb of a large nematoceran fly on a leaf of *D. margaritacea* (*D.* section *Arachnopus*), the limb donor successfully escaped; **e** leaf beetle (Coleoptera, Chrysomelidae) captured by *D. cucullata*, one autotomised limb is visible to the right (marked with red arrow), used for identification by DNA metabarcoding (Barcode Index Number: BOLD:AAH0483); **f** autotomised hind leg of an orthopteran on a leaf of *D. fragrans* (*D.* section *Arachnopus*), the limb donor apparently successfully escaped; **g** autotomised limb of *Aedes camptorhynchus* (Diptera, Culicidae) on a leaf of *D. zigzagia* (*D.* section *Ergaleium*), the limb donor successfully escaped, used for identification by

DNA metabarcoding (Barcode Index Number: BOLD:ACB5426); **h** autotomised limb of *Dilophus* (Diptera, Bibionidae) on a leaf of *D. rupicola* (*D.* section *Ergaleium*), the limb donor successfully escaped, used for identification by DNA metabarcoding (Barcode Index Number: BOLD:AAG6655); **i** autotomised limb of a crane fly (Diptera, Tipulidae) on the leaf of *D. huegelii* (*D.* section *Ergaleium*), the limb donor apparently successfully escaped; **j** a crane fly (Diptera, Tipulidae) captured by two leaves of *D. huegelii*, this individual had no autotomised limbs; **k** spider captured by *D. cucullata* with at least one autotomised limb. **a–c**, **e**, **f**, **k** from Theda Station, Western Australia; **d** from near Broome, Western Australia; **g**, **h** from near Hyden, Western Australia; **i**, **j** from near Donnybrook, Western Australia. Scale bars = 1 mm. Pictures: T. Krueger



**Fig. 2** Frequency distribution of number of autotomised limbs per observed case of autotomy in *Drosera* prey from Western Australia and the Northern Territory; results from 21 different species of *Drosera* and 80 total observed cases of autotomy

## Discussion

Our observations provide strong evidence that limb autotomy is employed by several groups of insects and spiders to aid escape when captured by *Drosera*. However, the success rate of this strategy appears to be relatively low, given that in almost two-thirds (64%) of observed cases the limb donor remained captured by the leaf on which its autotomised limbs were found in close proximity (see Fig. 1a–c for an example of such an unsuccessful escape attempt). In some cases, it is possible that the limb donor was absent due to other reasons, e.g. because it was washed away by rain or stolen by kleptoparasites (prey theft by kleptoparasites and opportunistic predators is common in *Drosera*, especially caused by ants, and it can account for up to 71% loss of captured prey of rosetted species; Thum 1989, Fleischmann et al. 2016). However, little to no rainfall was observed in the preceding four days for at least 25 of the 29 cases where the limb donor was absent (<http://www.bom.gov.au/climate/maps/rainfall>, accessed 10 May 2023).

Escape likelihood appears to decrease markedly with increasing number of limbs autotomised, indicating that this strategy is probably most successful when only a small number of legs (and none of the rest of the arthropod body) have come into contact with adhesive mucilage. Escaped insects with multiple autotomised limbs likely suffer from reduced fitness due to compromised locomotion (Fleming and Bateman 2007) and increased susceptibility to both active predators (Bateman and Fleming 2006) and passive predators, such as sundews (Cross and Bateman 2018). It is important to note that an arthropod's ability to escape from sticky traps, as well as its escape time, is correlated

to body size but to a lesser degree also to the body surface entangled in the trap. This was evidenced for adhesive passive predators from carnivorous plant traps such as *Drosera* (Gibson 1991) and from spider webs (Nentwig 1982).

Legs of large nematoceran flies (large body-sized Diptera, probably primarily comprising the family Tipulidae) were by far the most commonly observed autotomised body parts on the leaves of *Drosera*, regardless of season or location, comprising 83% of all observed cases (Online Resource 1). This represents a disproportionately large percentage compared to the abundance of large nematoceran flies in the prey spectrum of *Drosera*; previous studies suggest large nematoceran flies comprise only ca. 2.5% of the identifiable prey in *D.* section *Arachnopus* (Krueger et al. 2020), whilst Verbeek and Boasson (1993) did not identify any Tipulidae amongst 3453 prey items captured by Western Australian species of *D.* section *Ergaleium* and *D.* section *Bryastrum*. Two studies of *Drosera* prey outside Australia found Tipulidae species amongst the captured insects, but at low percentage (Judd 1969; Sciligo 2009); however, most did not observe this family (Murza et al. 2006; Costa et al. 2004, Lekešyte et al. 2018) or did not further differentiate nematoceran Diptera (Achterberg 1973; Thum 1986). Tipulidae and other large nematoceran flies can relatively easily autotomise their legs, with a previous study finding 50% of Tipulidae with one leg experimentally fixed by clamping were able to free themselves within one hour (Nentwig 1982). In addition, the characteristic anatomy of large nematoceran flies—a relatively large, slender, body with exceptionally long legs which can keep the thorax, abdomen, and wings far away from the sticky *Drosera* tentacles for an extended period of time (see Fig. 1j)—may contribute to the ability of members of this family to use autotomy to escape capture from *Drosera*. Long, slender legs have been shown to help other insects such as Dicyphina (Hemiptera, Miridae) to avoid entrapment by sticky plants (Wheeler and Krimmel 2015). By comparison, smaller nematoceran Diptera, such as Cecidomyiidae, Chironomidae, and Sciaridae, which represent some of the most common prey of erect *Drosera* species from Western Australia (Krueger et al. 2020, 2022; Verbeek and Boasson 1993) and globally (Judd 1969; Thum 1986; Murza et al. 2006; Costa et al. 2004) are often quickly and completely enveloped (including their wings) by the sticky mucilage, rendering any escape attempts impossible. The tentacle movement of most *Drosera* which increases mucilage contact with captured prey usually occurs within a few minutes after prey contact (Darwin 1875; Williams 1976; Poppinga et al. 2018). This tentacle reaction is positively correlated with the body size and movement of the captured prey, i.e. the larger and more struggling the insect that got stuck to the leaf, the more rapidly and strongly the tentacles will bend (Darwin 1875; Williams 1976).

Given the high frequency of the ability to autotomise limbs across arthropod orders and families (Fleming et al. 2007; Emberts et al. 2020), evidence for autotomy in arthropods captured by *Drosera* appears to be less common than one might expect (only 80 cases were found amongst > 10,000 *Drosera* leaves studied). This as noted may be due to most prey items being relatively small insects which become completely enveloped with mucilage before they can attempt to escape via autotomising limbs. Autotomised limbs were most commonly observed on the relatively large, narrowly linear-lanceolate leaves of species of *D.* section *Arachnopus*, which produce leaves typically ca. 5–15 cm in length (Krueger et al. 2020), compared with the much smaller, circular leaves of species from *D.* section *Ergaleium* (at least in the erect species), *D.* section *Lasiocephala*, and *D.* section *Bryastrum*, the sticky leaf surface of which is usually smaller than 1 cm in diameter (Lowrie 2014). Indeed, *Drosera* species that produce larger leaves tend to capture larger insects more frequently (Krueger et al. 2020), potentially explaining the relative abundance of autotomised large nematoceran fly limbs on species of *D.* section *Arachnopus*. Additionally, previous studies have also found significantly different prey spectra across different study sites, even for the same *Drosera* species, i.e. a locality effect which can only be explained by very different available prey at different sites (Lekesyte et al. 2018; Krueger et al. 2020). Little evidence for selective prey attraction has been observed in *Drosera* so far (Achterberg 1973; Thum 1986; Verbeek and Boasson 1993; Krueger et al. 2020), and the abundance of large nematoceran flies in the habitat thus likely strongly affects the incidence of autotomy in *Drosera* prey. A particularly notable example of this was a population of *D. huegelii* observed on 13 September 2020 near Donnybrook where Tipulidae were extremely abundant in the habitat; almost every plant had captured several Tipulidae as prey, despite this species having relatively small leaves (Fig. 1i, j).

## Conclusion

Limb autotomy is likely employed as a strategy by insects and other arthropods to escape capture by passive predators, such as *Drosera*. However, the low overall incidence of autotomy compared with studies of arthropod escape from other passive adhesive traps such as spider webs (Nentwig 1982) indicates that autotomy is a relatively rarely employed strategy for escape from *Drosera*. Our observations suggest that large nematoceran flies (comprised primarily of Tipulidae crane flies) most commonly employ this strategy when trapped by *Drosera* (which might explain why they are comparatively rare in the prey spectrum), potentially due to their large, slender body and very long limbs which often

prevent or delay decisive contact with the *Drosera* mucilage. Finally, we obtained compelling evidence that the likelihood of escape decreases markedly as multiple limbs are lost.

**Supplementary Information** The online version contains supplementary material available at <https://doi.org/10.1007/s11829-023-09978-5>.

**Acknowledgements** The Myers family and Dunkeld Pastoral supported fieldwork by the authors on Theda Station between 2011 and 2022, and Cecilia Myers and the staff of Theda Station are thanked for their hospitality and support. Jérôme Morinière and the AIM Lab (AIM—Advanced Identification Methods GmbH, Leipzig, Germany) are thanked for conducting the DNA metabarcoding and Axel Hausmann (ZSM, Munich) is thanked for assisting with sample preparation, both additionally helped with the barcode data. A flora-taking licence (FT61000038-2) was obtained for this project from the Western Australian Department of Biodiversity, Conservation and Attractions. Plant material was exported to Germany under an export permit (WT2020-001235) from the Australian Department of Agriculture, Water and the Environment. We also thank Eric LoPresti, Barry Rice and Dagmar Voigt for providing helpful comments on the manuscript.

**Funding** Open Access funding enabled and organized by Projekt DEAL. Thilo Krueger was supported by a Postgraduate Research Stipend Scholarship from Curtin University, Western Australia. Funding for metabarcoding was provided by the project “SNSB-Innovativ 2020” of the Staatliche Naturwissenschaftliche Sammlungen Bayerns SNSB (Bavarian Natural History Collections, Munich, Germany) to Andreas Fleischmann. Fieldwork in 2022 was supported by a 2019 research grant from the German Carnivorous Plant Society (G.F.P.) to Andreas Fleischmann and Thilo Krueger.

## Declarations

**Competing interest** The authors declare that they have no conflict of interest.

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