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2 **How dangerous is a *Drosera*? Limb autotomy increases passive predation risk in crickets**

3

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12

13 Short title: Autotomy and passive predation

14 **Abstract**

15 Autotomy, the voluntary shedding of body parts, is a strategy employed by many organisms  
16 to evade predation and escape entanglement. Although this strategy may allow an individual  
17 to survive one threat encounter it can come at significant cost, with studies indicating that  
18 autotomised individuals exhibit reduced fitness and increased susceptibility to active  
19 predators. However, little is known about the interplay between autotomy state and passive  
20 predation risk. We explored this interaction experimentally using prey of different size and  
21 autotomy state (laboratory-raised crickets) exposed to a sessile predator (the carnivorous  
22 plant *Drosera collina*). Data indicated a strong relationship between capture likelihood and  
23 autotomy state, with capture likelihood increasing from 6% in intact crickets (those retaining  
24 both hind legs) to 31% in single autotomised and 44% in double autotomised individuals. A  
25 weaker, though still strong, relationship was observed between capture likelihood and prey  
26 size, with smaller crickets (7–32 mg) paying a markedly greater cost for limb loss than larger  
27 crickets (100–280 mg). Capture likelihood for small crickets after single- or double-autotomy  
28 was increased by 56 and 72%, respectively compared to intact individuals, while this risk only  
29 increased by 2 and 13%, respectively for large crickets. Our results further highlight the costs  
30 of autotomy to fitness and the long-term survival of individuals, suggesting not only that this  
31 strategy may markedly increase the susceptibility of organisms to future passive predation  
32 but also that the cost is higher for earlier ontogenetic stages.

33

34 **Keywords:** *Acheta domesticus*, autotomy, carnivorous plant, passive predation, Orthoptera  
35 sessile predator,

36

37

## 38 **Introduction**

39 Autotomy is the voluntary shedding of parts of the body, usually as part of a defence tactic.  
40 Although perhaps the best known example is the shedding of tails by some species of lizards  
41 (see Arnold 1988; Clause and Capaldi 2006; Bateman and Fleming 2009 for reviews),  
42 autotomy is most common across invertebrate taxa. At least 200 invertebrate species are  
43 known to autotomise, and depending upon the organism multiple body parts can be shed  
44 including limbs, tails, caudal lamellae and mantles (see Fleming *et al.* 2007; Maginnis 2006a  
45 for reviews).

46

47 The adaptiveness of autotomy in invertebrates has been extensively studied, using  
48 orthopterans as a model taxon (e.g., Lagos 2017; Bateman and Fleming 2008). Studies indicate  
49 that while autotomy by orthopterans is adaptive, in that it allows an individual to escape  
50 predation (Bateman and Fleming 2006a), it also comes with a cost to locomotion (Bateman  
51 and Fleming 2011; Fleming and Bateman 2007; Hochkirch *et al.* 2002). Thus while autotomy  
52 may allow an organism escape from predation or entrapment, this survival can come at  
53 significant short-term (e.g., reduced speed, loss of specialised appendage or organ) and long-  
54 term (e.g., compromised feeding capability, reduced anti-predation or reproductive ability)  
55 cost (Fleming *et al.* 2007).

56

57 To date, studies considering the interplay between autotomy state and susceptibility to  
58 predators have been limited to actual or simulated active predators (Bateman and Fleming  
59 2006a, 2006b; Stoks 1998). However, entrapment and capture by sessile predators or other  
60 passive entrapments also likely represent threats to many invertebrates, and little attention  
61 has been paid to the role of autotomy state (i.e., being either intact or having undergone

62 autotomy) in increasing the risk of predation or entrapment from sessile threats. Examples of  
63 such threats include conspecifics - anemones (Cnidaria) autotomize tentacles when entangled  
64 with those of neighbours (Purcell 1977), commercial nets - crabs autotomizing limbs in  
65 commercial tangle-nets (Juanes and Smith 1995), and other non-predatory entanglements  
66 (Emberts *et al.* 2017), but also true passive predators such as the webs of spiders, the traps  
67 of sit-and-wait predators such as ant lions, and the trapping leaves of carnivorous plants.  
68 Many carnivorous plants are highly effective at trapping insect prey, particularly species from  
69 genera producing mucilaginous glandular appendages on leaf surfaces forming 'sticky' traps  
70 such *Byblis* (Byblidaceae), *Drosera* (Droseraceae), *Drosophyllum* (Drosophyllaceae),  
71 *Pinguicula* (Lentibulariaceae) and *Roridula* (Roridulaceae) (see for example Cross *et al.* 2018).  
72  
73 *Drosera* are the most iconic and diverse genus producing sticky traps, with over 250 species  
74 currently described and representatives occurring on every continent except Antarctica and  
75 in every climatic zone except the polar regions (Fleischmann *et al.* 2018). *Drosera* exhibit  
76 remarkable morphological diversity: from tiny rosetted species such as *D. pygmaea* from  
77 Australia and New Zealand which produces rosettes only 5 mm in diameter, to species with  
78 long (up to 30 cm) linear trapping leaves such as *D. filiformis* from North America or  
79 representatives of *D. sect. Arachnopus* from northern Australia, to large species such as *D.*  
80 *gigantea* which produces bushy growth to ca. 1 m x 0.5 m (Lowrie 2013; Fleischmann *et al.*  
81 2018). *Drosera* capture a wide spectra of prey ranging from small thrips to bees and even  
82 large dragonflies and lepidopterans (e.g., Murza *et al.* 2006; Cross *et al.* 2018; Fleischmann *et*  
83 *al.* 2018; Fig. 1a,b).

84

85 Although *Drosera* are evidently effective at capturing insect prey, the autotomised limbs of  
86 various arthropods are often observed on trapping leaves (A. Fleischmann and T. Krueger  
87 pers. obs.; see Fig. 1c), suggesting that at least some arthropods employ autotomy to escape  
88 entrapment by *Drosera*. If this is the case, then autotomy state is likely to significantly increase  
89 passive predation risk; individuals having already undergone autotomy would be at markedly  
90 greater risk of fatal entanglement than those able to undergo autotomy to escape. The aim  
91 of our study was to explore the interaction between autotomy state and passive predation  
92 risk, using laboratory-reared crickets (*Acheta domesticus*) of different size and autotomy  
93 state as prey and a rosetted *Drosera* species (*D. collina*) as a model sessile predator. We  
94 hypothesised that 1) passive predation risk (i.e., the likelihood of being fatally entangled)  
95 would decrease as prey size increased, with larger individuals less likely to be caught than  
96 smaller individuals; 2) that passive predation risk would increase with autotomy state  
97 regardless of prey size, with intact individuals (those retaining both hind legs) less likely to be  
98 caught than individuals having already lost one or both hind legs; and 3) that intact individuals  
99 would be more likely to exhibit autotomy as a strategy to escape entanglement than  
100 previously autotomised individuals.

101

## 102 **Materials and Methods**

### 103 *Study site and species*

104 We used a *Drosera* species, *D. collina* (N.G.Marchant & Lowrie) Lowrie (previously *D.*  
105 *erythrorhiza* subsp. *collina*) as the passive predator. This species exhibits a seasonal growing  
106 pattern typical of representatives from *Drosera* sect. *Ergaleium*, the most diverse group  
107 within the genus (ca. 70 species; Fleischmann *et al.* 2018). *Drosera collina* is a tuberous  
108 rosetted perennial (see Fig 2a) widely distributed in the Jarrah Forest of southwestern

109 Australia (Fig. 2a), producing large leafy rosettes up to 12 cm in diameter (Lowrie 2013) that  
110 are capable of trapping a diversity of ground-dwelling prey (Verbeek and Boasson 1993).  
111 To inform prey size classes for the autotomy experiment, preliminary field observations of *in*  
112 *situ* prey capture were undertaken for 58 *D. collina* individuals at a location in the Jarrah  
113 Forest east of Perth, Western Australia (GPS), in July 2017. Observations indicated that this  
114 species captured a similar spectrum of prey to that recorded previously for the closely related  
115 *D. erythrorhiza* (Verbeek and Boasson 1993; Dixon *et al.* 1980), predominantly small  
116 arthropods ranging from 1 mm to 1 cm in length (Table 1).

117

#### 118 *Autotomy experiment*

119 To test whether autotomy state increased passive predation risk in insects, juvenile  
120 laboratory-reared crickets (*Acheta domesticus*) were introduced to a potentially dangerous  
121 landscape simulating *D. collina* habitat following manipulated leg loss (Table 2). Leg loss was  
122 achieved by artificial mutilation of the entire hind leg at the trochanter. Groups of crickets  
123 from different size classes and autotomy states were introduced to a large pot (350 mm  
124 diameter, surface area 962 cm<sup>2</sup>) of which approximately 64% of the surface area was covered  
125 by the trapping leaves of *D. collina* (nine individuals covering ca. 615 cm<sup>2</sup>). The remaining  
126 surface area was open soil with a fine gravel layer. Cricket escape from the enclosure was  
127 prevented by a smooth wall of flexible plastic (20 cm high) secured around the rim of the pot.

128

129 The mass of all individual crickets was determined prior to experimentation (and after leg  
130 loss, where relevant), with cricket size classes chosen to reflect key juvenile life stages  
131 including nymphs, early moulting juveniles, and late moult pre-adults. All individuals were  
132 categorised as small (7–32 mg, mean  $17.8 \pm 1.0$  mg), medium (69–90 mg, mean  $78.9 \pm 0.6$  mg)

133 or large (100–280 mg, mean  $183.2 \pm 6.7$  mg). Autotomy states for each size class included  
134 individuals retaining both hind legs (intact), individuals with a single hind leg autotomised  
135 (single autotomised), and individuals with both hind legs autotomised (double autotomised).

136

137 Experimental treatments were conducted as sequential trials, with each trial comprised of 13  
138 intact crickets and 13 autotomised crickets introduced to the pot for a period of 24 hours. At  
139 the conclusion of each trial all crickets ('captured' or 'uncaptured') were removed, and *D.*  
140 *collina* individuals were allowed 24 hours to recover glandular secretions before the  
141 beginning of the next trial. A cricket was defined as 'captured' if it was completely entangled  
142 in mucilage and was either deceased or unable to move when gently contacted with forceps.

143

#### 144 *Statistical analyses*

145 To test the main and interaction effect of size class and autotomy state on susceptibility to  
146 capture in crickets, single- and multi-factor binary logistic regression models with a logit link  
147 function were fitted to binary capture data using size class and autotomy state (and the  
148 interaction between these factors) as categorical factors (SPSS Statistics 25, IBM, United  
149 States). Models employed wald  $\chi^2$  selection with indicator contrasts, and model selection was  
150 completed through minimizing the Akaike's Information Criterion (AIC). Predation risk for  
151 different size classes and different autotomy states was expressed as the odds ratio (*OR*). All  
152 data are presented as mean  $\pm$  1 s.e.

153

#### 154 **Results**

155 Autotomy state was a stronger predictor of capture likelihood (AIC = 17.8,  $\chi^2 = 28.1$ , df = 2, *P*  
156 <0.001) than was cricket size category (AIC = 18.0,  $\chi^2 = 20.5$ , df = 2, *P* <0.001), or a mixed

157 model including both factors and their interaction (AIC = 39.5,  $\chi^2 = 64.1$ , df = 8,  $P < 0.001$ ).  
158 Increasing autotomy state significantly increased passive predation in crickets for all size  
159 classes tested (Table 3). Across all size classes, capture likelihood increased from 6% in intact  
160 crickets to 31% in single autotomised and 44% in double autotomised crickets.

161

162 The mixed model indicated that there was a significant interaction between size class and  
163 autotomy state, driven by small\*single autotomy ( $P = 0.004$ ), small\*double autotomy ( $P =$   
164  $0.001$ ) and medium\*double autotomy ( $P = 0.042$ ). For small crickets, loss of a single leg  
165 increased predation risk by >50% ( $OR = 15.8$ ), and both legs by >70% ( $OR = 38.5$ ). For medium  
166 crickets, each leg lost increased predation probability by approximately 25% ( $OR$  not  
167 calculated as no intact crickets captured). Large crickets were only minimally effected by  
168 autotomy state, with the loss of a single leg only increasing predation chance by  
169 approximately 2% ( $OR = 1.4$ ) and both legs by just over 10% ( $OR = 4.6$ ).

170

171 Throughout the experiment there were no observations of crickets autotomising to escape  
172 capture by *D. collina* (i.e., no autotomised limbs were recorded from trapping leaves in any  
173 treatment).

174

## 175 **Discussion**

176 Our data indicate a strong relationship between passive predation risk and both autotomy  
177 state and the mass of prey individuals. Intact crickets retaining both hind legs of all size classes  
178 were less likely to be fatally entangled than were crickets that had undergone the loss of  
179 either one or both hind legs. However, this likelihood was markedly greater for crickets in the  
180 smallest size class; while large individuals paid virtually no predation-increase cost for the loss

181 of a single hind leg (2% increase in passive predation risk) and only a small cost for the loss of  
182 both hind legs (13% increase), the likelihood of capture by *Drosera* increased by 56% in small  
183 individuals after the loss of a single hind leg and by 72% after the loss of both hind legs. This  
184 indicates that the cost of autotomy may be significantly greater at earlier ontogenetic stages  
185 in species that are not able to regenerate their legs while undergoing the next instar stages;  
186 for small crickets, the elevated risk from even passive threats after the loss of even one hind  
187 leg may result in a lower probability of reaching reproductive maturity.

188

189 While the benefit of autotomy is obvious, allowing an individual to escape a threatening  
190 encounter with its life, the short- and long-term costs can be more difficult to quantify (Guffey  
191 1998; Fleming *et al.* 2007). With the exception of taxa with very different life stage  
192 morphologies and ecological niches, for example damselfly larvae that are able to autotomise  
193 caudal lamellae (Stoks *et al.* 1999; Stoks 1999; Stoks and De Block 2000), little is known about  
194 the differential cost of autotomy at earlier life stages. Autotomy at an early instar may induce  
195 rapid maturation at a smaller adult size, to reduce the costs of being autotomised (Matsuoka  
196 and Ishihara 2010). Research suggests that limb autotomy at nymphal stages come at a  
197 developmental cost for taxa able to regenerate lost limbs; for example, the stick insect  
198 *Sipoylidea sipylus* produces smaller wings and increased wing loading following limb loss and  
199 subsequent regeneration at juvenile instar stage (Maginnis 2006b). Similarly, limb autotomy  
200 can delay development in bush crickets (*Ephippiger ephippiger*) and locusts (*Locusta*  
201 *migratoria*) (Kubo *et al.* 1991; Lakes and Kalmring 1991). Reduced or otherwise compromised  
202 growth during final instars can permanently reduce adult body size, leading to decreased  
203 survival and fecundity in adult life stages (Juanes and Smith 1995; Stoks 1998). Loss of hind  
204 legs can compromise male mating ability in species such as the hemipteran bugs *Narnia*

205 *femorata* (Procter *et al.* 2012), particularly for species where hind legs are associated with the  
206 acoustic attraction of females (e.g., *Gryllus bimaculatus*; Bateman and Fleming 2005).

207

208 Our data show a marked increase in passive predation risk for autotomised individuals from  
209 earlier life stages, with ca. 30% of single autotomised and fewer than 15% of double  
210 autotomised nymphs surviving exposure to a passive threat. In contrast, survival rates were  
211 ca. 50% for early moulting juveniles and >80% for late moult pre-adults even after the loss of  
212 both hind limbs. If our data are reflective of natural conditions, autotomy at nymphal stage  
213 appears to come at the cost of a very low probability of survival to adult life stage.

214

215 Epigeic invertebrates are more commonly captured by prostrate and rosetted *Drosera*  
216 species, with volant invertebrates more frequently captured by species with upright and erect  
217 growth forms (Verbeek and Boasson 1993; Thum 1986). However, even rosetted *Drosera* such  
218 as *D. erythrorhiza*, closely related and similar in size and growth habit to *D. collina*, have been  
219 observed to trap prey as large as butterflies, dragonflies and grasshoppers (e.g., Dixon *et al.*  
220 1980). Despite little evidence of specific prey attraction cues in most *Drosera* (e.g., colour,  
221 nectar rewards or the production of volatiles; Jürgens *et al.* 2009; Cross *et al.* 2018; Horner *et*  
222 *al.* 2018), they are clearly effective sessile predators capable of successfully trapping even  
223 quite large insects. Subsequently, they are likely to represent a considerable passive  
224 predation threat to invertebrates in habitats where they occur in large numbers. Although  
225 field observations of prey capture in *D. collina* did not record any trapped representatives  
226 from the Gryllidae, juvenile crickets fall within the size spectra for prey captured by *D. collina*  
227 and thus we consider it a suitable model organism to test the proposed hypotheses.

228

229 This study employed laboratory-reared *Acheta domesticus* as a test organism, with leg loss  
230 manipulated experimentally. However, our treatments are comparable to the range of  
231 natural autotomy patterns exhibited by wild populations of the related cricket species *Gryllus*  
232 *bimaculatus*. Approximately 39% of *G. bimaculatus* individuals sampled from natural  
233 populations exhibited limb autotomy, most commonly the loss of one or both hind legs  
234 (Bateman and Fleming 2005). Similarly, in wild populations, cave cricket *Hadonoecus*  
235 *subterraneus* are more often missing hind legs than other legs and between 6% and 40% of  
236 individuals have lost at least one leg (Chandoo *et al.* 2013). Therefore, we are confident that  
237 our experimental design reflects natural patterns of autotomy states within invertebrate  
238 populations.

239

240 Future studies should consider the behaviour of potential prey in the context of passive  
241 predation risk. Although we did not consider the behaviour of studied crickets in this  
242 experiment, we observed that immediately after release into the experimental enclosure  
243 crickets typically explored the soil surface before seeking shelter beneath the leaves of the  
244 *Drosera*. In this manner initial capture rates may have been high, with surviving individuals  
245 simply avoiding capture by remaining stationary. In another studied system of a sessile plant  
246 predator and its prey, presence of the aquatic carnivorous plant *Utricularia vulgaris* did not  
247 influence spatial distribution or behaviour of its zooplankton prey (Englund and Harms 2001).  
248 However, it is evidenced that invertebrate prey, including crickets, can learn to avoid  
249 predatory cues (Kortet and Hedrick 2004). This may be the case with *Drosera* and its prey.

250

251 This study further highlights the cost of autotomy in invertebrates, and suggests that earlier  
252 ontogenetic stages may pay a higher price for the loss of even a single limb. Future studies

253 should focus on the differential cost of autotomy at different ontogenetic stages in greater  
254 detail, for both vertebrates and invertebrates.

255

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389

390 **Figure captions**

391

392 **Figure 1.** *Drosera* capture a wide spectrum of prey from small thrips and flies (*D. erythrorhiza*,  
393 A) to large insects such as dragonflies (*D. serpens*, B). Autotomised insect limbs and wings are  
394 often observed on the trapping leaves of *Drosera* (*D. capensis*, C). Image credits AT Cross (A),  
395 T Krueger (B) and A Fleischmann (C).

396

397 **Figure 2.** Growth habit (A) and typical Jarrah Forest habitat (B) of *Drosera collina*. Image  
398 credits PW Bateman.

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