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Source: Florida Entomologist, 91(1) : 126-127

Published By: Florida Entomological Society

URL: https://doi.org/10.1653/0015-4040(2008)091[0126:AIASII]2.0.CO;2

AUTOTOMY IN A STICK INSECT (INSECTA: PHASMIDA): PREDATION VERSUS MOLTING

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Autotomy, or appendage loss, is common in many animals, including reptiles, amphibians, mammals, birds, fish, echinoderms, crustaceans, spiders, and insects (see Maginnis 2006a; Fleming et al. 2007 for reviews). In arthropods, there are 2 hypotheses for this phenomenon. First, limbs may be lost through predation attempts; if a predator were to grab a leg instead of the body, the animal can shed the leg and flee to escape predation (McVean 1982; Carlberg 1986; Formanowicz 1990; Robinson et al. 1991). And second, limbs can be shed during complications with molting. As a result of having a skeleton on the outside of the body, arthropods must repeatedly shed their old exoskeleton and replace it with a new one. During this complicated process, jointed appendages can become stuck in the old cuticle and must be shed to survive (Bedford 1978; Foelix 1982; Carlberg 1986; Robinson et al. 1991; Brock 1999).

Although many taxa within the phylum Arthropoda experience autotomy, Phasmida is the only order within the class Insecta that regularly sheds and regenerates lost legs (Borrer et al. 1992). As such, it is important to identify the selective pressures for autotomy in this group. In the laboratory, legs are lost to molting complications approximately 30% of the time (Maginnis 2006b). In the field, a sampled population showed approximately 40% of individuals with missing or regenerated legs (Maginnis & Maginnis 2007). However, these rates offer no insight into the selective pressures behind autotomy. The goal of this study was to determine the effects of predation attempts and/or molting complications on rates of leg loss in a population of *Didymuria violescens*, the spur-legged phasmatid, native to south eastern Australia (Campbell & Hadlington 1967).

Because it is impossible to control molting complications, 'predator-free' environments were created in Bago State Forest, New South Wales, Australia. Ten eucalyptus trees (*Eucalyptus radiata*, their food source)—all approximately 7 m high and 68 centimeters in diameter breast height (DBH)—were covered in mosquito netting. Before sealing each tree, all visible animals were manually removed and 25 first instars were subsequently placed in each tree (for a total of 250 individuals). The sexes of this species were indistinguishable at this time, so no effort was made to perform the experiment with an equal number of males and females. Individuals were kept contained until maturity (approximately 3 months later), at which time they were removed and inspected for leg loss and/or evidence of regeneration. Nymphs always commence regeneration after autotomy, and regenerated legs are always smaller than non-regenerated legs (Bordage 1905; Ramme 1931; Carlberg 1992; Maginnis 2006b).

The results revealed that 17.3% of adults within the predator-excluded trees were missing and/or regenerated at least one leg during development ($n = 112$; 4 of the 10 trees were destroyed by cattle (100 individuals), 29 individuals died, 6 individuals were still nymphs, and 3 individuals were unaccounted for (original $n = 250 - 100 - 29 - 6 - 3 = 112$). This suggests that both predation attempts and complications with molting play important roles as causes of autotomy in this population. Interestingly, the rate of autotomy and/or regeneration in the enclosed trees, presumably free from predation, was nearly half of the observed rate in a sampled 'natural' population (~40%, same species and study location, Maginnis & Maginnis 2007). This might suggest that ~20% of individuals in a phasmid population experience complications with molting at some point during their lifetime, and predation attempts double that base rate of autotomy. That is, perhaps half of the cases of autotomy might be due to molting complications, and half might be due to predation. It is also worth noting that atypical predation attempts could have taken place in this experiment; the "anti-predation" design in this study was aimed at organismal predators such as birds and mantids, yet legs could have been lost to the viscous surface of fresh sap flows within the enclosed trees.

While there is little doubt that all arthropods capable of autotomy experience high selective pressure due to predation, 2 factors make the cause of autotomy in stick insects particularly interesting. First, their overall shape; their long and thin legs that are so effective at conferring crypsis could lead to higher rates of molting complications than arthropods with shorter, stouter legs. Second, their exceptional crypsis may lead to higher rates of 'misses'; a well camouflaged prey item, a predator might easily mistake a leg for a body, and thus lead to more missed predation attempts relative to other less well camouflaged animals.

In conclusion, recognition of the selective pressures of autotomy on phasmids may provide insight as to why they are the only order of insects that regularly shed and regenerate lost legs. This, in combination with future work on the developmental mechanisms and tradeoffs associated with autotomy and regeneration, promise to bring a better understanding of this phenomena.

I thank Lawrence Maginnis and the late Alex Marshall for help collecting these data, and Dr. Allan Hook for assistance with an earlier version of this manuscript. This research was funded by the National Science Foundation (DIG# 0309038).

SUMMARY

Autotomy is common in many arthropods, and can be due to predation avoidance and/or complications during molting events. This study evaluated the effects of both on rates of leg autotomy in a population of *Didymuria violescens*, the spur-legged phasmatid. The results suggest that in natural habitats, these insects experience leg loss due to molting complications approximately 20% of the time.

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