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# Restio culm felling is a consequence of pre-dispersal seed predation by the rodent *Rhabdomys pumilio* in the Fynbos

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ABSTRACT

Seed mortality represents a substantial cost for plants and can have a large effect on plant reproductive fitness. Here we report evidence for pre-dispersal seed mortality by a novel mechanism: culm felling in female nut-seeded restios by rodents. We noted strong female-specific culm felling in the nut-fruited *Cannomois congesta* Mast. (Restionaceae) from the South Western Cape, South Africa. Camera-trap analysis showed that this culm felling is carried out by the striped mouse, *Rhabdomys pumilio* Spar. (Muridae) and is primarily aimed at obtaining ripe seeds held at the tips of female culms rather than eating the culm. All seeds acquired by *R. pumilio* were found to be consumed. We recorded a mean loss of 81% culms/seeds in affected female *C. congesta* plants in contrast to very few culm losses from males. This highly selective rodent behaviour is presumably due to detectable differences in the nutritional reward associated with terminal male/female inflorescences (large nut-like seeds vs. pollen). Pre-dispersal seed predation through culm felling could significantly reduce the fecundity of ant-dispersed restios such as *C. congesta* because fewer seeds manage to fall to ground where mutualistic ground foraging ants compete with rodents for seeds. Culm losses through felling could also have physiological and nutritional implications. Future research should explore the generality of this phenomenon amongst the Restionaceae, and quantify the associated physiological and reproductive costs.

## 1. Introduction

Plant reproductive fitness is largely determined by the successful production, dispersal and germination of seeds. Seed production represents a substantial cost for a plant yet plants are forced to produce large quantities of seed to secure a relatively small number of successfully germinated seedlings, primarily due to extensive seed mortality (Crawley, 2000). The largest contributors to seed mortality are pre and post-dispersal seed predation by animals (Janzen, 1971). Because of the large quantities of seed produced by plants, a relatively small change in percentage seed mortality due to predation can lead to a large difference in the number of seeds which germinate and can have significant effects on plant population dynamics (Crawley, 2000).

The intense pressure of seed predation is hypothesised to have led to the evolution of many interesting strategies which plants use to ensure the successful recruitment of seedlings. These include hard seed coats (Paulsen et al., 2014), camouflage (Nystrand and Granström, 1997; Porter, 2013), producing satiating quantities of seed (Vander Wall, 2010), producing secondary compounds (Xiao et al., 2008) and even the use of animals to aid in the dispersal of seeds to safe sites.

In the South Western Cape of South Africa, many large-seeded Restionaceae species in the genera *Cannomois, Hypodiscus, Hypolaena, Restio and Willdenowia* are myrmecochorous (having seeds which are dispersed by ants) (Bond and Slingsby, 1983). Ground foraging ants are attracted by elaiosomes (a fatty-lipid reward attached to myrmecochorous seeds) causing them to move and bury the seeds, where they consume only the elaiosomes and leave the seeds ‘planted’ underground. (Marloth, 1915; Slingsby, 1981; Bond and Breytenbach, 1985). More recently it has been shown that some large seeded restios are also scatter hoarded by small mammals (Midgley et al., 2002) and some are even dispersed by dung-beetles (Midgley et al., 2015).

Seed depot experiments with myrmecochorous seeds have shown strong competition between small mammals and ants for access to seeds fallen to ground (Bond and Breytenbach, 1985; Heithaus, 1981; Christian and Stanton, 2004). Seed predation by Cape rodents can be as high as 100% however the presence of ant-dispersers reduces this percentage significantly (Bond and Breytenbach, 1985). Ants normally respond rapidly after seed-fall and bury seeds underground where rodents struggle to locate them (Heithaus et al., 1980; Heithaus, 1981). The removal of the elaiosomes by ants decreases the likelihood of a rodent subsequently digging up a seed after it has been buried by

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ants (Bond and Breytenbach, 1985; Christian and Stanton, 2004). The process of myrmecochory has been hypothesised to have evolved due to the necessity for large seeds to escape intense small-mammal seed predation (Giladi, 2006).

However, predation of myrmecochorous seeds before seed-fall, would effectively exclude mutualistic ants from the competition for seeds thus eliminating them as potential seed-dispersers. This could have significant effects on nut-fruited restio populations which may be solely dependent on the process of myrmecochory for successful seed dispersal. Pre-dispersal seed predation could indicate intense competition between ants and small mammals for access to myrmecochorous seeds causing rodent seed predation to pre-empt seed-fall.

Here we document a previously unrecorded rodent behaviour of culm felling in a dioecious nut-fruited Cape Restionaceae, *Cannomois congesta* Mast. Following field observations of significant female-specific culm-removal in *C. congesta*, we asked the following questions: 1) were culms consumed (herbivory) or felled from the plants (i.e. vegetative tissue not consumed) 2) was culm-removal biased toward female *C. congesta* plants 2) what was the agent causing culm felling 3) what was the fate of seeds on felled culms? Using vegetation surveys, camera trapping and seed depot experiments, we showed that culms were indeed felled and not consumed, that this culm felling was limited to female plants, was conducted by the rodent *Rhabdomys pumilio* Spar. (Muridae), and resulted in pre-dispersal seed mortality that could compromise the efficacy of the myrmecochorous seed dispersal strategy.

## 2. Methods

### 2.1. Study site

Our study site was located at Jonaskop (−33° 94′ 16 S 19° 52′ 52 E) in the South Western Cape of South Africa. Jonaskop is dominated by cold wet winters and hot dry summers, typical of the South Western Cape. The surrounding vegetation was sparse, low Fynbos contrasted by dense stands of mature *Protea repens* L. (Proteaceae). The most recent fires were at least 15 years prior to this investigation and vegetation was mature. The soils at the site were shallow and rocky and are derived from quartzitic sandstone (Agenbag, 2006).

### 2.2. Investigating the culm-felling phenomenon

To determine whether culms were felled rather than consumed in female *C. congesta* plants, the mean length of felled culm fragments was added to the mean length of remaining culm-stumps on plants and then compared to the mean length of intact, mature female culms. Inflorescences were not included in the intact culm length measurements as they were missing from the majority of culm fragments. A *t*-test was used to test for significant differences between the mean length of the culm fragments plus culm stumps and the mean length of intact mature female culm length.

To quantify the extent of culm-felling in *C. congesta* plant canopies, the ratio of felled:living:senescent culms within the canopy was measured for both sexes. Felled:living:senescent ratios included culms which had senesced or been felled (culm stumps) over the years prior to the study because dry culm material persisted in canopies. Male and female *C. congesta* plants were measured in 4 m × 12 m transects. Counting all culms and assigning them to groups was not possible due to their high numbers. Thus, a plastic ring with a circumference of 6.5 cm was used to sub sample the culms throughout the canopy of each plant (six sub samples for each individual plant). In each sub sample, the number of living, felled and senescent culms was carefully counted. The ratio of felled:living:senescent culms was averaged from the six sub samples, giving a ratio of felled:living:senescent culms for each plant.

Data were analysed using the software package R. To statistically analyse culm state differences in the canopies, felled:living:senescent ratios were treated as compositional data because proportions summed to one. According to this method, felled:living:senescent ratio data were converted into compositional data, which was then run through a MANOVA. Converting to compositional data was necessary because ratio data violate the ANOVA assumption of independence of variables. The data conversion method followed is described in full in Van der Boogaart and Tolosana-Delgado (2006).

### 2.3. Recording culm-felling in C. congesta females using camera traps

Starting in August 2014, before any sign of recent culm-felling activity, two terminal inflorescences were selected in each of seven *C. congesta* females and baited with a mixture of peanut butter and oats in order to test the hypothesis that rodents are the cause of the culm-felling phenomenon. Peanut butter and oats can be used as an effective bait to attract rodents (e.g. Anderson and Ohmart, 1977). This was done in order to increase the chances of recording the phenomenon, assuming the rodents would attempt to acquire the bait in the same way they would acquire an inflorescence holding ripe seeds. Baited culms were monitored from late afternoons through late mornings, using Little Acorn (Ltl-5210A) camera traps (supplied by the Biological Sciences Dept. UCT). Cameras were pointed to the base of targeted female restios and set to low sensitivity due to the amount of culm movement in the wind. Once triggered cameras were set to record a two minute video and take still photographs. This experiment was carried out over three day periods each month until October. During these experiments, un-baited female culms were also monitored with camera traps in the hope of catching the phenomenon without the use of bait. Un-baited females were monitored until late December.

### 2.4. The fate of C. congesta seeds

During November 2014, *C. congesta* seeds were collected on site using nylon bags, which were tied around the terminal inflorescences of selected bunches of mature, female culms. Ten tagged seeds were placed out at each of six stations beneath restios, 40 m apart. Stations were monitored continuously using Little Acorn (Ltl-5210A) camera traps. Cameras were pointed toward seed depots on the ground and set to high sensitivity. Cameras were set to record a two minute video and take still photographs. Tagging consisted of gluing 25 cm lengths of UV thread (fly-fishing backing line) to the husks of viable seeds which allowed seed displacement to be tracked using UV torches after dark. Non-toxic UV powder (radiantcolor.com) was also scattered around the seed depot to assist in tracking small mammal movements. The UV powder was able to stick to the feet of small mammals for a short duration revealing the direction of their movements. Stations were replenished with tagged seeds after 24 h. This experiment was carried out twice, the 6th–8th November 2014 and 29th–30th December 2014.

## 3. Results

### 3.1. Culm-felling of female C. congesta plants

Initial field observations lead us to strongly suspect a rodent seed predator as the cause of strikingly different female/male *C. congesta* canopy structures at Jonaskop (Fig. 1A, B). A large proportion of female plants had culms which were diagonally cut mid-way along the culm (Fig. 1A, C). In contrast, culms on male plants persisted until complete senescence (Fig. 1B). The cut halves of female culms did not appear to have been eaten and formed a skirting of dry culm fragments scattered around the base of female plants (Fig. 1D). The inflorescences were largely destroyed or missing on the fallen female culm fragments (Fig. 1D).